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A New Species of the Genus *Parachremylus* Granger (Hymenoptera: Braconidae), a Parasitoid of *Conopomorpha* Lychee Pests (Lepidoptera: Gracillariidae) in Thailand

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Abstract.—***Parachremylus litchii* Belokobylskij & Maeto, new species**, from Thailand is described as a parasitoid of larvae of *Conopomorpha sinensis* Bradley and *C. litchiella* Bradley, the major pests of lychee and longan in South-East Asia. The taxonomic position of *Parachremylus* and the range of the hosts of related genera of parasitoids are discussed.

Several insect pests are seriously threatening lychee (*Litchi chinensis* Sonn.) and longan (*Dimocarpus longan* Lour.) (Sapindaceae) growers. They are the fruit borer (*Conopomorpha sinensis* Bradley), leaf miner (*Conopomorpha litchiella* Bradley), longan sucking bug (*Tessaratoma papillosa* Drury), fruit piercing moth (*Othreis fullonia* (Clerck)), and twig borer (*Zeuzera coffeae* Nietner) (Menzel 2002).

Conopomorpha sinensis, the lychee stem-end borer and the lychee fruit borer in China, Thailand and India, is the major pest of lychee and longan in these countries. *Conopomorpha sinensis* and the related *C. litchiella* both attack lychee and longan, the latter preferring to mine leaves and shoots (Bradley 1986). There have been only tentative reports on braconid parasitoids of the pest *Conopomorpha* borers: *Phanerotoma* sp., *Pholetesor* (*Apanteles*) sp., and *Colastes* sp. (Menzel 2002, Anupunt and Sukhvibul 2005), but possibly information about *Colastes* is due to misdetermination. Here we report a new braconid of the genus *Parachremylus* Granger as a larval parasitoid of *C. sinensis* and *C. litchiella*.

The genus *Parachremylus* with type species *P. seyrigi* Granger was originally described from Madagascar (Granger 1949); this genus occurrs also in continental Africa—Nigeria and Niger (Wharton 1993). Two additional species of this genus have already been recorded from the Oriental region. *Parachremylus oblongus* (Papp) was described from India in the genus *Avga* Nixon (Papp 1990, 1997), and *P. temporalis* Belokobylskij from Brunei (Belokobylskij 1999). A fourth species of this genus, similar to *P. temporalis*, is described below from Thailand. The systematic position of this genus is disputable. *Parachremylus* is included in the subfamily Exothecinae (tribe Avgini: Belokobylskij 1993), or conventionally in subfamily Hormiinae (Wharton 1993). In spite of the different understanding of the contents of subfamilies, the position of this genus close to *Avga* Nixon is suggested by both authors. Belokobylskij (1993) discussed the relationships of these genera with *Parahormius* Nixon, *Pseudohormius* Tobias & Alexeev and *Allobracon* Gahan (= *Leurinion* Muesebeck), which share the loss of the prepectal (epicnemial) carina on the

mesosoma. Wharton (1993) provisionally placed *Avga* near *Parahormius* and *Pseudohormius* and showed the possible relationship of *Avga* and *Parachremylus* (shared granulate mesonotal sculpture and the poorly developed propleural flange). However, in his opinion, *Allobracon* does not appear to be closely related to *Parachremylus* in spite of it sharing a number of features with *Avga* and *Parahormius*.

The host of *Parachremylus* has not been known till now. The new species described below as *P. litchii* sp. nov. was reared from larvae of *Conopomorpha sinensis* and *C. litchiella* (Gracillariidae), both important pests of lychee and longan trees in South-East Asia. The members of related genera of the tribe Avgini (*Parahormius, Avga, Allobracon*) are also recorded as parasitoids of the leaf-rollers or leaf-miners of the families Tortricidae, Gracillariidae, Lyonetiidae, Cosmopterigidae, Coleophoridae, and Gelechiidae (Belokobylskij 1993, Wharton 1993) as well as rarely (recorded for *Allobracon*) of leaf-mining Coleoptera (Wharton 1993).

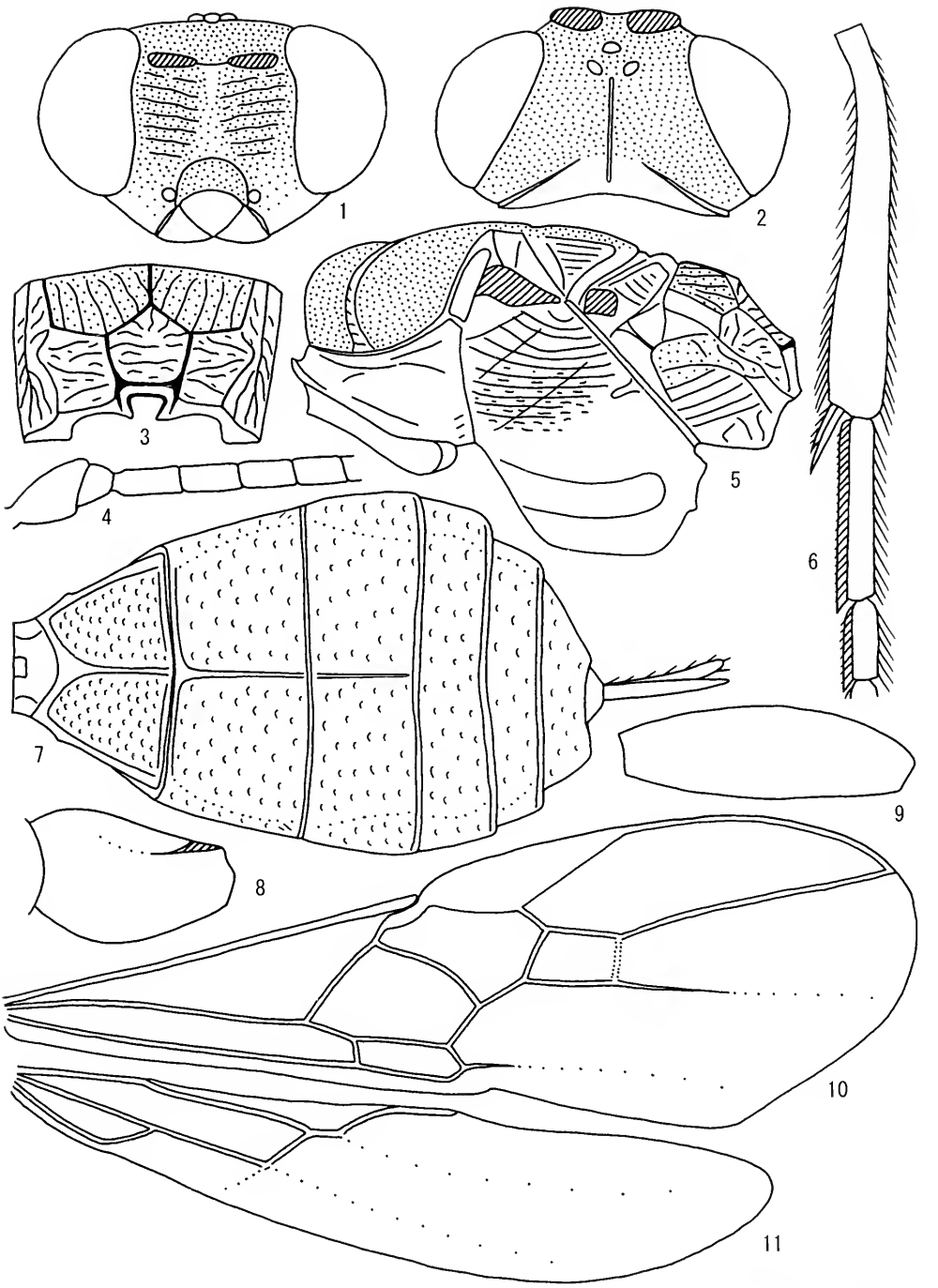
The terms of wing venation are used as defined by Belokobylskij and Tobias (1998). The following abbreviations are used: POL—postocellar line; OOL—ocular-ocellar line; Od—maximum diameter of lateral ocellus; NIAES—National Institute of Agro-Environmental Sciences (Tsukuba, Japan); ZISP—Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia).

Parachremylus litchii Belokobylskij & Maeto, new species

(Figs 1–11)

Holotype female.—"Horticultural Research Center, Chiang Rai, Thailand, viii, 1996, Supatra Dolsopon", "Host: *Conopomorpha litchiella* larvae on Lychee or Longan" (NIAES). Paratypes. 2 females, 1 male, with the same labels as holotype (NIAES, ZISP); 5 females, "Horticultural Research Center, Chiang Rai, Thailand, 6. vi, 1997, Supatra Dolsopon", "Host: *Conopomorpha sinensis* larvae" (NIAES, ZISP).

Description.—Female. Body length 2.6–2.8 mm; fore wing length 2.5–2.6 mm. *Antennae*: thickened, almost filiform, 29–30-segmented, 1.1–1.2 times longer than body. Scapus 1.7–2.0 times longer than wide. First flagellar segment 2.5–2.8 times longer than its apical width, 1.1–1.2 times longer than second segment. Penultimate segment 2.0–2.3 times longer than wide, 0.6–0.7 times as long as first flagellar segment, 0.7–0.75 times as long as apical segment; the latter with distinct spine apically. *Head*: width 1.8–2.0 times its median length, 1.25–1.4 times width of mesoscutum. Temple very strongly and almost linearly narrowed behind eye (dorsal view). Transverse diameter of eye (dorsal view) 5.5–7.0 times longer than temple length (7.0–7.7 times if measured on straight line). Ocelli small, in triangle with base 1.1–1.15 times its sides. POL 0.7–1.0 times Od, 0.3–0.5 times OOL. Vertex with narrow median longitudinal furrow. Occipital carina dorsally distinctly curved towards ocelli, rather widely interrupted medially; not fused with hypostomal carina ventrally being obliterated for a short distance. Eye large, sub-round, glabrous, 1.1–1.2 times as high as broad. Malar space 0.25–0.3 times height of eye, 0.8–0.9 times basal width of mandible. Face width 0.9 times height of eye and 1.2–1.25 times height of face and clypeus combined. Malar suture absent. Clypeal suture rather distinct and complete. Clypeus weakly convex. Hypoclypeal depression subround, its width 0.8–0.9 times distance from edge of depression to eye, 0.35 times width of face. Head below eyes (front view) strongly and almost linearly narrowed. *Mesosoma*: length 1.5–1.55 times its height. Mesoscutum highly and almost perpendicularly raised above pronotum (lateral view), with rather fine longitudinal medioposterior keel (dorsal view). Notauli rather narrow, shallow anteriorly on vertical surface and very shallow to almost



Figs 1–11. *Parachremylus litchii* sp. nov. 1, Head, frontal view. 2, Head, dorsal view. 3, Propodeum. 4, Six basal segments of antenna. 5, Mesosoma, lateral view. 6, Hind tibia and two basal segments of hind tarsus. 7, Metasoma, dorsal view. 8, Hind coxa. 9, Hind femur. 10, Fore wing. 11, Hind wing.

absent on dorsal surface, finely sculptured. Prescutellar depression short, shallow, finely crenulate-granulate, 0.15–0.2 times as long as scutellum. Scutellum almost flat. Metanotum medially with small and obtuse tubercle. Subalar depression rather shallow, wide, densely and curvedly striate with fine granulation anteriorly. Sternauli shallow, rather wide, weakly curved, entirely smooth. *Wings*: Length of fore wing 2.8–3.0 times its maximum width. Radial cell not shortened, metacarpus 1.3 times longer than pterostigma. Pterostigma rather wide, 3.1–3.7 times longer than wide. Radial vein arising a little or rather distinctly before middle of pterostigma. Second radial abscissa 1.5–2.3 times longer than first abscissa, 0.25–0.3 times as long as the straight third abscissa, 1.15–1.25 times longer than the weakly curved first radiomedial vein. Second radiomedial cell short, weakly narrowed towards apex, its length 1.5–1.8 times maximum width, 0.9–1.1 times length of brachial cell. First medial abscissa rather distinctly S-shaped. Recurrent vein 0.9–1.0 times as long as second abscissa of medial vein. Discoidal cell 1.55–1.65 times longer than wide. Nervulus strongly postfurcal, distance from nervulus to basal vein nearly twice nervulus length. Parallel vein arising a little behind middle of distal margin of brachial cell. Hind wing 4.5–4.7 times longer than maximum width. First abscissa of costal vein 0.85–0.9 times as long as second abscissa. First abscissa of mediocubital vein 1.15–1.2 times longer than second abscissa. Recurrent vein short, unsclerotized, interstitial, curved toward base of wing. *Legs*: Hind coxa large, 1.5–1.6 times longer than wide, 0.7–0.75 times as long as hind femur. Hind femur wide, 3.1–3.2 times longer than wide. Hind tibia thickened towards apex. Hind tarsus 1.1 times longer than hind tibia; hind basitarsus 0.6–0.65 times combined length of second-fifth segments (without pretarsus). Second tarsal segment 0.4–0.45 times as long as basitarsus, 1.2–1.3 times longer than fifth segment (without pretarsus). First-fourth segments of hind tarsus ventrally with wide and transparent flanges, which are pointed on the tops of each segment. *Metasoma*: 1.7–2.0 times longer than its maximum width, 0.9–1.1 times as long as head and mesosoma combined. First tergite strongly, uniformly and linearly widened from base to apex; with small spiracular tubercles before its middle; laterally with distinct high and rather wide carinae; fine dorsal carinae fused in basal 0.3 and then extending to apex as a single, elevated, median carina; dorsope absent. Apical width of first tergite 2.4–2.7 times its basal width; its length 0.6–0.65 times apical width. Second suture rather distinct and convex. Second and third tergites with rather distinct and fine longitudinal median carina. Median length of second tergite about half its basal width, equal to or 1.1–1.2 times length of third tergite. Combined median length of second and third tergites nearly equal to basal width of second tergite, 0.7–0.75 times maximum width of tergites. Ovipositor sheath (visible part in lateral view) 1.1–1.3 times longer than first tergite, 1.0–1.2 times longer than hind basitarsus, 0.25–0.4 times as long as mesosoma, 0.15–0.17 times as long as fore wing. *Sculpture and pubescence*: Head very densely and minutely granulate, face additionally with rather fine and irregular striation. Mesoscutum very densely and distinctly granulate, with rather narrow and long rugulosity in medioposterior half. Scutellum finely and densely granulate. Mesopleuron almost smooth in lower half. Metapleuron coarsely, regularly and curvedly striate for the most part, with fine granulation between striae and anteriorly. Propodeum almost entirely coarsely and rather sparsely striate, striae in areola more or less transverse and partly undulate or rugulose, with fine granulation partly; with distinctly delineated basolateral areas; areola wide, its length 1.0–1.2 times maximum width; dorsal carina 0.8–1.0 times as long as areola fork. Hind coxa smooth; hind femur finely punctulate with

very fine granulation dorsally, smooth ventrally. Metasoma entirely densely granulate, granulation becoming finer towards apex of metasoma. Mesoscutum entirely shortly and very densely setose. Hind tibia dorsally with rather short, dense and semi-erect setae, its length 0.35–0.55 times maximum width of tibia. *Colour*: Head and anterior half of mesosoma (including mesoscutum) yellow, posterior part of mesosoma and metasoma pale yellow, metasoma additionally often with greenish tint. Antenna reddish brown or brown, scapus mostly yellow. Palpi pale yellow. Legs yellow, all tarsi (especially posterior ones) more or less brown. Ovipositor sheath brown in basal half and black in apical half. Fore wing faintly infuscate. Pterostigma brownish yellow.

Male.—Body length 2.0 mm; fore wing length 2.4 mm. Head width 2.1 times its median length. Transverse diameter of eye (dorsal view) 8.8 times longer than temple length if measured on straight line. Antenna 28-segmented. Otherwise similar to female.

Diagnosis.—The new species is very similar to *P. temporalis* Belokobylskij from Brunei (Belokobylskij 1999) and differs in having the recurrent vein as long as second abscissa of medial vein, the nervulus strongly postfurcal, the pterostigma rather wide, the hind femur wide, the second tergite short, the face rather finely striate, and the propodeum almost entirely coarsely rugose-striate.

Host.—*Conopomorpha sinensis* Bradley and *C. litchiella* Bradley (Gracillariidae).

Distribution.—Thailand.

Etymology.—This species is named after the name of the fruit tree—lychee (*Litchi chinensis* Sonn.)—on which their hosts develop.

KEY TO SPECIES OF THE GENUS *PARACHREMYLUS* GRANGER

1. Temple longer; transverse diameter of eye (dorsal view) 4.0–5.0 times as long as temple length. Malar space larger than basal width of mandible. Mesopleuron smooth in upper half, striation partly present in subalar depression only. 1st–4th segments of hind tarsus with narrow and partly indistinct flanges 2

- Temple shorter; transverse diameter of eye (dorsal view) 5.5–7.0 times as long as temple length. Malar space less than basal width of mandible. Mesopleuron distinctly curvedly striate in upper 0.4–0.5. 1st–4th segments of hind tarsus with wide flanges 3

2. Notauli complete, rather deep posteriorly. Metacarpus 1.2–1.3 times as long as pterostigma. 1st flagellar segment 3.5–3.7 times as long as apical width. Median length of 2nd and 3rd metasomal tergites combined a little larger than basal width of 2nd tergite. Propodeum mostly coarsely and sparsely striate. Body length 2.2 mm.—Madagascar ***P. seyrigi* Granger**

- Notauli incomplete, almost absent posteriorly. Metacarpus 1.5 times as long as pterostigma. 1st flagellar segment 3.0 times as long as apical width. Median length of 2nd and 3rd metasomal tergites combined 1.3 times basal width of 2nd tergite. Propodeum mostly smooth. Body length 2.0 mm.—India ..... ***P. oblongus* (Papp)**

3. Pterostigma narrow, 5.0 times as long as maximum width. Recurrent vein of fore wing about twice as long as second abscissa of medial vein. Nervulus not strongly postfurcal, distance from nervulus to basal vein 0.7 times nervulus length. Hind femur 3.5 times as long as wide. 2nd tergite 0.6 times as long as its basal width. Face almost entirely distinctly transversely striate. Propodeum within background areolation sparsely striate, mostly smooth. Body length 2.3 mm.—Brunei ..... ***P. temporalis* Belokobylskij**

- Pterostigma rather wide, 3.1–3.7 times as long as maximum width. Recurrent vein of fore wing almost as long as second abscissa of medial vein. Nervulus strongly postfurcal, distance from nervulus to basal vein nearly twice nervulus length. Hind femur 3.1–3.2 times as long as wide. 2nd tergite about 0.5 times as long as its basal width. Face finely and partly indistinctly transversely striate and with dense fine granulation. Propodeum within background areolation almost entirely coarsely rugose-striate with fine granulation partly. Body length 2.0–2.8 mm.—Thailand ..... ***P. litchii* sp. nov.**

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Parasitoids (Hymenoptera: Chalcidoidea) of the Cabbage Seedpod Weevil (Coleoptera: Curculionidae) in Georgia, USA

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Abstract.—Five families and 13 species of Chalcidoidea (Hymenoptera) were obtained from mass-reared seedpods of *Brassica napus* L. (Brassicaceae) as putative parasitoids of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), in Georgia, USA. The species are *Conura torvina* (Cresson) (Chalcididae), *Euderus glaucus* Yoshimoto and *Necremnus tidius* (Walker) (Eulophidae), *Brasema allynii* (French) **n. comb.** (from *Eupelmus* Dalman) and *Eupelmus cyaniceps* Ashmead (Eupelmidae), *Eurytoma tylodermatis* Ashmead (Eurytomidae), and *Lyrcus incertus* (Ashmead), *L. maculatus* (Gahan), *L. perdubius* (Girault), *Mesopolobus moryoides* Gibson, *Neocatolaccus tylodermae* (Ashmead), *Pteromalus cerealellae* (Ashmead) and *Pteromalus* sp. (Pteromalidae). An illustrated key is provided to differentiate the taxa. *Lyrcus maculatus* constituted about 96% of all reared Pteromalidae and 86% of the total parasitoid fauna. The associations of *B. allynii*, *E. glaucus*, *E. cyaniceps*, *E. tylodermatis*, *L. incertus*, *N. tylodermae*, *Pteromalus* sp. and *P. cerealellae* with *C. obstrictus* are new, but some of these species likely are hyperparasitoids or emerged from insect contaminants of the mass-reared seedpods. The only previous report of a parasitoid of *C. obstrictus* in eastern North America, *Trichomalus perfectus* (Walker) (Pteromalidae), is a misidentification. The parasitoid fauna of *C. obstrictus* in Georgia is discussed relative to that known for western North America.

The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), was introduced from Europe to western North America about 70 years ago. Since then it has become the most important insect pest of canola and rape, *Brassica napus* L. and *B. rapa* L. (Brassicaceae), in most areas of the continent where these crops are grown (Cárcamo et al. 2001, Kuhlmann et al. 2002). It was first reported from eastern North America in North Carolina, USA (USDA 1960), and is now known to extend from Georgia to Quebec and Ontario, Canada (Brodeur et al. 2001, Mason et al. 2004). There have been several surveys of the introduced and native chalcid (Hymenoptera: Chalcidoidea) parasitoids of the cabbage seedpod weevil in western North America, including Breakey et al. (1944), Doucette (1944, 1948), Hanson et al. (1948), Carlson et al. (1951), McLeod (1953), Walz (1957), and Dosdall et al. (in press). Murchie and Williams (1998) listed 7 identified and 4 unidentified species in 9 genera and 5 families of Chalcidoidea as parasitoids of *C. obstrictus* in North America, but almost all of the species names either represent misidentifications or are now recognized as junior synonyms of older names (Gibson et al. 2005). Dosdall et al. (in press) reported another six chalcid species as reared from *B. napus* and *B. rapa* seedpods in Alberta. Consequently, the

Table 1. Chalcid parasitoids associated with the cabbage seedpod weevil in North America, including for Georgia the number of specimens and percentage (in parenthesis) of total parasitoids reared by Buntin (1998).

Taxon	Western North America	Georgia
Chalcididae		
Conura albifrons (Walsh)	+	–
? *Conura side* (Walker)[1]	+	–
Conura torvina (Cresson)	+	9 (0.8)
Eulophidae		
Euderus albitarsis (Zetterstedt)	+	–
Euderus glaucus Yoshimoto	–	2 (0.2)
Necremnus tidius (Walker)	+	6 (0.5)
Eupelmidae		
Brasema allynii (French)	–	5 (0.5)
Eupelmus cyaniceps Ashmead	–	4 (0.4)
Eupelmus vesicularis (Retzius)	+	–
Eurytomidae		
Eurytoma tylodermatis Ashmead	+	25 (2.2)
Pteromalidae		
Chlorocytus sp.	+	–
Lyrcus incertus (Ashmead)	–	6 (0.5)
Lyrcus maculatus (Gahan)	+	967 (86.0)
Lyrcus perdubius (Girault)	+	60 (5.3)
Mesopolobus bruchophagi (Gahan)	+	–
Mesopolobus mayetiolae (Gahan)	+	–
Mesopolobus moryoides Gibson	+	2 (0.2)
Neocatolaccus tylodermae (Ashmead)	–	33 (2.9)
Pteromalus cerealellae (Ashmead)	–	1 (0.1)
Pteromalus spp.[2]	+	4 (0.4)
Trichomalus lucidus (Walker)	+	–

[1] Single record, likely a misidentification of *C. torvina* (see text).
[2] Females in the two regions represent different species (see text).

chalcid fauna purportedly parasitizing *C. obstrictus* in western North America includes at least 14 species (Table 1). In contrast, there is only a single published report of parasitoids of *C. obstrictus* in eastern North America. Buntin (1998) stated that greater than 96% of the parasitoids recovered from seedpods of *B. napus* in Georgia were *Trichomalus perfectus* (Walker) (Pteromalidae). This species is the most common biological control agent of *C. obstrictus* in Europe (Murchie and Williams 1998) and was long thought to have been introduced to North America along with the seedpod weevil. However, Gibson et al. (2005) showed that all previous reports of *T. perfectus* in western North America were misidentifications of *Trichomalus lucidus* (Walker), another European species.

Accurate identification of parasitoid species is a prerequisite for successful classical biological control and integrated pest management. The senior author examined the parasitoids reared by Buntin (1998) as part of a larger study to document the diversity and identity of the chalcid parasitoids of *C. obstrictus* in North America. The primary purpose of Buntin (1998) had been to examine the effect of trap cropping on the number of seedpod weevils and its parasitoids in canola crops in Georgia. The species identities of the parasitoids had therefore never been thoroughly investigated. The purpose of this paper is to provide the first comprehensive information on the diversity of the chalcid parasitoids reared from canola seedpods in southeastern USA in order to facilitate future studies of the parasitoid fauna associated with *C. obstrictus* throughout North America.

MATERIALS AND METHODS

The chalcid parasitoids identified in this study were obtained from mass-reared seedpods of *B. napus* collected from the Bledsoe Research Farm (33 10.635'N 84 24.354'W) located near Griffin, Georgia, from 1994–1996, as per "Material and methods" in Buntin (1998). Although not stated, the pods were screened for insect contaminants prior to rearing. Contaminants mainly included aphids (Hemiptera:

Aphididae) and larvae and pupae of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). The reared parasitoids had been stored in ethanol, but were critical-point dried, point-mounted, and identified to genus by the senior author using the relevant family keys in Gibson et al. (1997). The senior author is responsible for all species identifications except *Eurytoma tylodermatis* Ashmead (Eurytomidae), which was identified by MWG. Information concerning the method of species identification within each genus is provided under the relevant species discussion. Voucher specimens are deposited in the Canadian National Collection of Insects and Arachnids (CNC), Ottawa, Ontario, the University of Georgia Museum of Natural History (UGCA), Athens, Georgia, and the United States National Museum of Natural History (USNM), Washington, District of Columbia. Terms used for parasitoid structure follow Gibson (1997). Photographs are composite serial images that were combined using Auto-Montage™. These images and the scanning electron microphotographs were digitally retouched using Adobe Photoshop™ to enhance clarity.

RESULTS

A total of 1,127 specimens of Chalcidoidea were sufficiently intact that they could be identified accurately. Of these, there was a single male *Pachyneuron aphidis* (Bouché) and a female and male *Asaphes suspensus* (Nees) (Pteromalidae). Members of *Pachyneuron* and *Asaphes* are obligate hyperparasitoids of aphids (Gibson et al. 1997) and are not dealt with further. The remaining 1,124 specimens included 5 families, 10 genera, and 13 species of Chalcidoidea that are possible parasitoids of *C. obstrictus*. These taxa are keyed below and subsequently treated by family in alphabetical order. The key also segregates *Trichomalus* Thomson and *Chlorocytus* Graham, the only two genera reared from *C. obstrictus* in western North America (Dosdall et al. in press) that were not recovered by Buntin (1998) (Table 1). The two taxa are included in the key because species of both genera occur in eastern North America and may eventually be reared as part of the regional *C. obstrictus* parasitoid fauna.

KEY TO CHALCIDOIDEA PUTATIVELY PARASITIZING *C. OBSTRICTUS* IN GEORGIA

1 Hind leg with elongate coxa of similar length to conspicuously swollen and ventrally toothed femur, and with curved tibia (Fig. 1) ... *Conura torvina* (Cresson) (Chalcididae)

\- Hind leg with comparatively short coxa, slender femur, and straight tibia (Figs 3–8) ... 2

2(1) Tarsi 4-segmented; flagellum with 3 or 4 funicular segments, the segments sometimes branched (Figs 9, 10) ..... (Eulophidae) 3

\- Tarsi 5-segmented; flagellum with 5 or 6 unbranched funicular segments (Figs 11–18) ... 4

3(2) Meso- and metatarsi with basal 4 segments white; forewing membrane bare dorsally behind marginal vein, but with clearly visible row of long admarginal setae (Fig. 42, ams) on ventral surface near marginal vein; flagellum of both sexes with 4 unmodified funicular segments ..... *Euderus glaucus* Yoshimoto

\- Meso- and metatarsi with basal 1 or 2 segments white; forewing membrane uniformly setose dorsally behind marginal vein, the setae largely obscuring admarginal setae on ventral surface (Fig. 41); flagellum branched in male (Fig. 10) and with only 3 funicular segments in female (Fig. 9) ..... *Necremnus tidius* (Walker)

4(2) Head and mesosoma with coarse piliferous punctures and non-metallic, dark brown to black (Figs 3, 4); pronotal collar quadrangular in dorsal view, only slightly shorter than mesoscutum; male with elongate petiole and flagellar segments having whorls of conspicuously long setae (Fig. 4).....

. . . . . *Eurytoma tylodermatis* Ashmead (Eurytomidae)

- Head and mesosoma with finer mesh-like sculpture and often with metallic green to bluish luster; pronotum strongly transverse in dorsal view, conspicuously shorter than mesoscutum; male with short petiole and flagellar segments having short, inconspicuous setae 5

5(4) Mesopleuron elongate, convex or cushion-like, and uniformly finely sculptured (Figs 5, 7); middle leg with strong black spines at apex of tibia and on ventral surface of tarsal segments (Figs 5, 7, sp), the colour of spines contrasting distinctly with mostly yellowish leg . . . . . (Eupelmidae: Eupelminae female) 6

- Mesopleuron about as high as long, usually with a smooth region dorsally below base of wings and often with an oblique femoral depression or groove, but at least not convex or uniformly sculptured (Figs 23–25); middle leg with slender spines at apex of tibia and on ventral surface of tarsal segments, the colour of spines not contrasting with leg 7

6(5) Ovipositor sheaths projecting only slightly beyond apex of gaster and uniformly coloured (Fig. 5); forewing completely setose behind parastigma and marginal vein (Fig. 5) . . . . . *Brasema allynii* (French)

- Ovipositor sheaths projecting beyond apex of gaster by about one-third its length and medially whitish between darker basal and apical bands (Fig. 7); forewing with slender, oblique bare band (Fig. 7, bb) below parastigma and base of marginal vein . . . . . *Eupelmus cyaniceps* Ashmead

7(5) Flagellum with only basal segment conspicuously differentiated as strongly transverse ring segment and with 7 or 8 distinct funicular segments; head in frontal view with inner margin of eyes distinctly divergent over about ventral half; mesotibial spur much longer and thicker than metatibial spurs, as long as basal tarsal segment and about one-third length of tarsus . . . . . (Eupelmidae: Eupelminae male) 8

- Flagellum with 2 or 3 basal segments conspicuously differentiated as ring segments and then with 6 or 5 tubular funicular segments, respectively (Figs 11–18); head in frontal view with inner margin of eyes subparallel or slightly but uniformly incurved; mesotibial spur somewhat longer than, but otherwise similar to, metatibial spurs, the spur obviously shorter than basal tarsal segment and only about one-quarter length of tarsus . . . . . (Pteromalidae) 9

8(7) Forewing completely setose behind parastigma and base of marginal vein (Fig. 6); hind leg with femur yellowish-white and tibia usually more or less distinctly brown (Fig. 6); flagellum clavate, the segments widening distinctly to clava and apical funicular segments transverse (Fig. 6) . . . . . *Brasema allynii* (French)

- Forewing with large, oblique bare region (Fig. 8, bb) behind parastigma and base of marginal vein; hind leg with femur and tibia dark (Fig. 8); flagellum robust-filiform, the segments all about the same width and apical funicular segments quadrate (Fig. 8) . . . . . *Eupelmus cyaniceps* Ashmead

9(7) Flagellum with 5 tubular funicular segments and 3 strongly transverse ring segments (Figs 11, 13, 14) 10

- Flagellum with 6 tubular funicular segments and 2 ring segments (Figs 12, 15–18) . . . 14

10(9) *Female only*: head and mesosoma dark with conspicuous, white, lanceolate setae (Figs 19, 20, 24, 25); costal cell ventrally with setae only within about apical half of cell (Figs 43, 46) 11

- *Female or male*: head and mesosoma variable in colour, but with inconspicuous hairlike setae (Figs 21–23); costal cell ventrally with line of setae extending almost entire length of cell or at least setae present both basally and apically if line more or less interrupted medially (Figs 44, 45) 13

11(10) Forewing dorsally setose behind marginal vein over about apical half of vein, the setae partly obscuring at least 3 rows of ventral admarginal setae apically (Fig. 43); propodeum with transverse ridge or carina within anterior half dividing it into anterior and posterior sections on either side of median carina (Fig. 30);

metapleuron completely sculptured and with anterior margin on same plane as and abutting mesopleuron (Fig. 25, am) ..... *Neocatolaccus tylodermae* (Ashmead)

- Forewing dorsally bare behind marginal vein to level at least equal with middle of stigmal vein, completely exposing 1 or sometimes 2 partial rows of ventral admarginal setae (Fig. 46, ams); propodeum sometimes with transverse furrow near middle, but without transverse ridge (Figs 27, 29); metapleuron partly smooth anteriorly and with anterior margin either curved outward (Figs 24, 29) or extending anteriorly above and over posterior margin of mesopleuron (Figs 27, 28) 12

12(11) Propodeum with nucha (Fig. 29, nuc) delineated laterally by longitudinal carina within furrow along posterior margin; metapleuron with anterior margin (Figs 24, 29, am) curved outwards, extending as thin brown flange almost at right angle to posterior margin of mesopleuron; lower face without evident malar depression, evenly convex along oral margin between malar sulcus and clypeus ..... *Lyrcus perdubius* (Girault)

- Propodeum with nucha not delineated laterally by carina, the furrow along posterior margin of callus continued uninterrupted mesally and anteriorly so as to delineate, more or less conspicuously, anterior limit of nucha (Fig. 27); metapleuron with anterior margin (Figs 27, 28, am) raised above and extending over posterior margin of mesopleuron; lower face with short but distinct, concave malar depression (Fig. 20, md) between malar sulcus and clypeus ..... *Lyrcus incertus* (Ashmead)

13(10) *Both sexes*: mesonotum usually dark with conspicuous pattern of bluish-green spots, the spots usually most distinct on mesoscutum paramedially behind pronotum and laterally on lateral lobe adjacent to notaulus, though small specimens sometimes brown. *Female*: gaster lanceolate (Fig. 22); forewing dorsally bare behind marginal vein to level at least equal with middle of stigmal vein (Fig. 45). *Male*: flagellum brown with first funicular segment oblong and much longer than combined length of the 3 ring segments (Fig. 14); marginal vein strong, but only as thick as width of stigma and with posterior margin straight, parallel with anterior margin..... *Lyrcus maculatus* (Gahan)

- *Both sexes*: mesonotum metallic green. *Female*: gaster subcircular (Fig. 21); forewing dorsally bare behind marginal vein, but apically the setae extending to base of stigmal vein (Fig. 44). *Male*: flagellum yellowish with first funicular segment quadrate to slightly wider than long and at most as long as combined length of the 3 ring segments (Gibson et al. 2005, fig. 8); marginal vein conspicuously thickened relative to slender stigma and with posterior margin slightly convex (Gibson *et al.* 2005, fig. 31) ..... *Mesopolobus moryoides* Gibson

14(9) *Male only*: forewing with bare band behind marginal vein extending to level about equal with middle of stigmal vein, and with 1 or at most 2 partial rows of admarginal setae (Fig. 46, ams) that are obviously longer than setae on dorsal surface of disc; metapleuron partly smooth and with anterior margin (Figs 24, 28, am) curved outward or raised above mesopleuron 15

- *Male or female*: forewing with bare region behind marginal vein less extensive, the discal setae extending to or almost to base of stigmal vein, and with more than 2 rows of admarginal setae of about same length as setae on dorsal surface of disc (Figs 43, 47–50); metapleuron completely sculptured and with anterior margin (Fig. 25, am) on same plane as and abutting mesopleuron 16

15(14) Propodeum with nucha (Fig. 29, nuc) delineated laterally by longitudinal carina within furrow along posterior margin; flagellum with most funicular segments only slightly longer than wide, the first segment subquadrate and shorter than pedicel (Fig. 15); metapleuron with anterior margin (Figs 24, 29, am) curved outwards, extending as thin brown flange almost at right angle to posterior margin of mesopleuron ..... *Lyrcus perdubius* (Girault)

- Propodeum with nucha not delineated laterally by carina, the furrow along posterior margin of callus extending uninterrupted mesally and anteriorly so as to delineate, more or less conspicuously, anterior limit of nucha (Fig. 27); flagellum with all funicular segments clearly oblong, the first segment as long as pedicel (Fig. 16); metapleuron with anterior margin (Figs 27, 28, am) raised above and extending anteriorly over posterior margin of mesopleuron ..... *Lyrcus incertus* (Ashmead)

16(14) *Male only*: head and body dark with conspicuous, long, slightly lanceolate white setae (Fig. 25); propodeum with transverse ridge or carina within anterior half dividing it into anterior and posterior sections on either side of median carina (Fig. 30) ..... *Neocatolaccus tylodermae* (Ashmead)

- *Male or female*: head and body metallic green with inconspicuous hairlike setae (Fig. 26); propodeum with or without median carina but without transverse ridge (Figs 35–38) 17

17(16) Pronotum anteriorly with collar rounded into neck, the reticulations extending uninterrupted from dorsal to inclined surface (*cf.* Figs 23, 24); forewing with marginal vein comparatively short, less than 1.5 times as long as stigmal vein (Figs 49, 50); propodeum with convex, reticulate nucha (Figs 31, 32, nuc), reticulate panels (Figs 31, 32, pnl), and often without distinct median carina 18

- Pronotum anteriorly with shiny, transverse carina differentiating collar from neck (Fig. 26); forewing with marginal vein obviously (at least 1.5 times) longer than stigmal vein (Figs 47, 48); propodeum with flat or slightly concave, lunate or triangular adpetiolar strip (Fig. 35, aps) delineated by inverted Y-shaped median carina anterior to petiolar foramen or, if with reticulate nucha (Fig. 37, nuc), then with panels (Fig. 37, pnl) partly strigose (having oblique, irregular, fine carinae or striae) 19

18(17) *Female*: costal cell with line of setae on ventral surface interrupted medially (Fig. 49); scutellum anterior to frenum with reticulations distinctly smaller medially than laterally (Fig. 33); propodeum with plical carina (Fig. 31, pc) directed obliquely toward inner margin of spiracle ..... *Pteromalus cerealellae* (Ashmead)

- *Female*: costal cell with entire line of setae ventrally (Fig. 50); scutellum anterior to frenum with almost uniform meshlike reticulations (Fig. 34); propodeum with plical carina (Fig. 32, pc) less strongly angled, directed distinctly mesal of inner margin of spiracle toward outer margin of basal fovea (Fig. 32, bf) ... *Pteromalus* sp.

19(17) Metacoxa setose dorsally only over about apical half; forewing of female without setae on basal fold (Fig. 48); propodeum with inverted Y-shaped median carina delimiting adpetiolar strip (Fig. 35, aps); propodeum in male without complete plical carina (Fig. 36, pc) and in female largely bare posterior to spiracle, setose only from callus to postspiracular sulcus (Fig. 35, pss) ..... *Chlorocytus* Graham[3]

- Metacoxa setose dorsally over at least apical two-thirds and often completely setose to base; forewing of female with at least a couple of setae on basal fold (Fig. 47, bf) differentiating basal cell from speculum; propodeum with or without median carina but with convex, reticulate nucha (Fig. 37, nuc); propodeum in male with complete plical carina (Fig. 38, pc) and in female extensively setose posterior to spiracle, from callus to complete, strong plical carina (Fig. 37) ..... *Trichomalus* Thomson[3]

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[3] Genus not yet reported parasitizing *C. obstrictus* in eastern North America.

SPECIES NOTES, ARRANGED BY FAMILY

Chalcididae

One species of Chalcididae was reared—*Conura torvina* (Cresson), which comprised nine specimens (7 ♀♀, 2 ♂♂) or 0.8% of the parasitoid fauna. Delvare (1992) keyed the species-groups of *Conura* and differentiated *C. torvina* as one of eight species of the *side*-group in a key to the "common species" of that group in North America north of Mexico. Prior to Delvare (1992), *C. torvina* was consistently misidentified as *Conura side* (Walker). Carlson et al. (1951) reported that a specimen of *C. side* was reared from *C. obstrictus* in California. We were unable to locate this specimen to confirm the identification, but it is possible that it is conspecific with the Georgia species because *C. torvina* is transcontinental in North America (Delvare 1992, Noyes 2002). Because of the confusion in names prior to Delvare (1992), the list of published distribution and host records given for *C. side* by Noyes (2002) certainly contains many records that actually refer to *C. torvina*. Based on previous name usage, of those Curculionidae listed as hosts of *C. side* by Noyes (2002), the record of the cotton boll weevil, *Anthonomus grandis* (Boheman), probably does refer to *C. side*, whereas the records of *Rhynchaenus pallicornis* (Say) and *Hypera* spp. likely refer to *C. torvina*. Because of variability in the colour pattern features given by Delvare (1992), females of *C. torvina* can be easily misidentified as *Conura albifrons* (Walsh), another transcontinental species that Dosdall et al. (in press) reported parasitizing *C. obstrictus* in Alberta. Females of both species have paramedial yellow marks on the first gastral tergum, but in female *C. torvina* the distance between the marks is, at most, only about equal to the length of a mark (Fig. 2). In female *C. albifrons* the separation between the marks is at least similar to the width of a mark, if not conspicuously greater. Males of the two species are more easily differentiated. Males of *C. torvina* have the interantennal region and lower face yellow, whereas males of *C. albifrons* have the clypeus dark so that they have a conspicuous, angulate (∧-like), yellow band extending dorsally between the antennal scrobes.

Eulophidae

Two genera and species of Eulophidae were reared—*Euderus glaucus* Yoshimoto (2 ♀♀; 0.2% of the parasitoid fauna) and *Necremnus tidius* (Walker) (1 ♀, 5 ♂♂; 0.5% of the parasitoid fauna). Although *E. glaucus* was known from Florida and Texas (Noyes 2002), its association with *C. obstrictus* in Georgia represents a new state distribution record and a possible new host record. The only other reported host for *E. glaucus* is *Epiblema obfuscana* (Dyar) (Lepidoptera: Tortricidae) (Yoshimoto 1971). Dosdall et al. (in press) reported a second *Euderus* species, *E. albitarsis* (Zetterstedt), as an incidental parasitoid of *C. obstrictus* in Alberta, but this association was also obtained by mass-rearing seedpods. *Euderus glaucus* and *E. albitarsis* are differentiated in Yoshimoto (1971), though problems remain in species recognition within the genus.

Necremnus tidius is a comparatively common parasitoid of *C. obstrictus* in western North America, but it was misidentified as *N. duplicatus* Gahan prior to Gibson et al. (2005), who differentiated and illustrated the species. The specimens from Georgia represent the first record of the species in eastern North America.

Eupelmidae

Two genera and species of Eupelmidae were reared—*Eupelmus* (*Eupelmus*) *cyaniceps* Ashmead (2 ♀♀, 2 ♂♂; 0.4% of the parasitoid fauna) and *Brasema allynii* (French) **n. comb.** (from *Eupelmus* Dalman) (1 ♀, 4 ♂♂; 0.5% of the parasitoid fauna). *Brasema* Cameron is unrevised for the region, but there are about 25 described species in North America north of Mexico.

Most of the species are currently misclassified in *Eupelmus* (Gibson 1995). Gahan (1933) described and partly illustrated both sexes of *B. allynii* as a parasitoid of the Hessian fly, *Mayetiola destructor* (Say) (Diptera: Cecidomyiidae). Phillips and Poos (1921) also provided both a dorsal and lateral habitus of the female, and for both sexes illustrated the colour pattern of the legs, important species-recognition features, when they described the immature stages of *B. allynii* as a parasitoid of the wheat jointworm, *Tetramesia tritici* (Fitch) (Hymenoptera: Eurytomidae). The sexes of Eupelminae are strongly dimorphic (Gibson 1995), but the more important diagnostic features of *B. allynii* females include: head and mesosoma variably brown or dark with metallic green luster, scrobal depression finely coriaceous and quite shiny, lower face with relatively sparse and only inconspicuously lanceolate white setae, mesonotum finely coriaceous, and middle legs entirely or largely yellow beyond coxae (mesofemur and tibia often with some light brown infusion but mesofemur not extensively dark). Males of *B. allynii* are in part diagnosed within *Brasema* by a clavate flagellum with very short and inconspicuous setae (Fig. 6), head and mesosoma metallic green, head with only very slightly lanceolate and comparatively sparse white setae, and legs with all femora yellow (Fig. 6). *Brasema allynii* is transcontinental in North America and a polyphagous primary or facultative hyperparasitoid of hosts in concealed situations. Noyes (2002) listed 58 host species in 22 families of Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera, though the putative host record of *C. obstrictus* is the first for Curculionidae.

Gibson (1995) recognized three subgenera in *Eupelmus*, including *E.* (*Episolindelia*) Girault and *E.* (*Macroneura*) Walker in addition to the nominate subgenus. Noyes (2002) listed 45 valid species of *Eupelmus* in the Nearctic region, but this includes all three subgenera and several species incorrectly classified to genus. *Eupelmus* is unrevised for the region, but there are about 15 described species of *E.* (*Eupelmus*) in North America north of Mexico. *Eupelmus cyaniceps* belongs to the *urozonus* species-group *sensu* Gibson (1995). Hunter and Pierce (1912, pl. XVIII, f) provided a dorsal habitus drawing of the female when they recorded the species as a parasitoid of *A. grandis*. A species revision of *E.* (*Eupelmus*) that includes evaluation of size-correlated and host-induced variation is necessary to confidently characterize species limits within the subgenus. However, females of *E. cyaniceps* are differentiated from most other regional species of the subgenus by the following combination of features: macropterous, the forewing hyaline and with a linea calva (Fig. 7, bb), scape dark, mesosoma dark with metallic green luster, and ovipositor sheaths extending for a distance at least equal to two-thirds length of the metatibia and with a medial white band (Fig. 7). Because of extreme sexual dimorphism (*cf.* Figs 7, 8), species recognition in *Eupelmus* is based almost entirely on females; males are not characterized for most species. The features provided in the key for males of *E. cyaniceps* are of family and generic level. *Eupelmus cyaniceps* is a primary or facultative hyperparasitoid of hosts in concealed situations. The rearing from *C. obstrictus* represents a new putative host record, but Noyes (2002) listed 17 other species in 11 different genera of Curculionidae as part of 65 host records in 20 families of Coleoptera, Diptera, Hymenoptera and Lepidoptera.

The only eupelmid previously reported as a parasitoid of *C. obstrictus* is *Eupelmus* (*Macroneura*) *vesicularis* (Retzius) from Washington state (Hanson et al. 1948) and British Columbia (McLeod 1953). This species likely represents one of the earliest accidental introductions from Europe to North America; only females are known in North America and they are brachypterous (Gibson 1990).

Eurytomidae

One species of Eurytomidae was reared —*Eurytoma tylodermatis* Ashmead, which comprised 25 specimens (8 ♀♀, 17 ♂♂) or 2.2% of the parasitoid fauna. The Georgia rearing represents a new host record for *E. tylodermatis*, but a previously unidentified species of *Eurytoma* was also reared in most surveys of the parasitoid complex of *C. obstrictus* in western North America (Doucette 1948, Hanson et al. 1948, McLeod 1953, Dosdall et al. in press). Examination of voucher and additional reared material from Alberta, British Columbia, Idaho, Oregon, and Washington indicates the western species is also *E. tylodermatis*. Noyes (2002) listed 19 other curculionid species in 11 genera as part of 46 reported host species in 14 families of Coleoptera, Diptera, Hymenoptera and Lepidoptera.

Over 90 nominal species of *Eurytoma* are known from the Nearctic region (Noyes 2002). Bugbee (1967) revised the North American species, but species recognition remains extremely difficult because of variability of the morphological features he used to differentiate species, and because sexual dimorphism (*cf.* Figs 3, 4) presents difficulties in recognizing conspecific sexes. Rearing is necessary to make the association, and one sex of several species of *Eurytoma* remains undescribed. Bugbee (1967) examined over 4,000 specimens originally identified as *E. tylodermatis* in the USNM and stated that "even this number was not enough to give an adequate picture of the geographical distribution, or the range of variation of several species in the complex" (Bugbee 1967, p. 492). He keyed *E. tylodermatis* as one of 48 species of his "*tylodermatis* complex" and considered the species to be most closely related to *E. bolteri* Riley, *E. diastrophi* Walsh, and *E. pini* Bugbee. He also stated that the four species were probably associated with the larvae of weevils and small moths that live in stems of various plants, either as primary parasitoids or as hyperparasitoids. It is beyond the scope of this study to assess the monophyly of species-groups or species limits in *Eurytoma*, but at least the four *Eurytoma* species listed above have the propodeum densely setose lateral to the propodeal foramen, and the petiole (Fig. 40, ptl) has one dorsomedial and two anterolateral processes. Furthermore, the anterior margin of the first gastral tergum (Fig. 40, Gt1) is emarginate and depressed medially, and the tergum is deeply depressed anterolaterally, to accommodate the processes of the petiole when the gaster is raised. Bugbee's (1967) key to species differentiates *E. tylodermatis*, in part, by stating the sculpturing of the fourth gastral tergum extends over the dorsal surface at least narrowly along the anterior margin (couplet 20). The species description, however, states that the sculpture of the fourth tergum is heavy ventrolaterally, continues dorsally for about one-half to two-thirds of the surface, and then fades out so that the dorsal surface is smooth and shiny. The extent of sculpturing on the fourth gastral tergum appears to be variable in species of *Eurytoma*, and the appearance is partly affected by telescoping of the terga. Features that can be used in combination to differentiate *E. tylodermatis* from similar species include the malar space lacking an alveolate boss (a slightly raised area), the ventrolateral margin of the scrobes (Fig. 39, vls) being produced anteriorly and reflexed posteriorly, and the median channel of the propodeum being distinct and defined laterally by carinae formed by longitudinally aligned crenulae (Fig. 40).

A single species of *Eurytoma*, *E. curculionum* Mayr, has also been reported as reared from *C. obstrictus* in Europe (Dmoch 1975). Individuals of *E. curculionum* have a mesocoxal lamella according to Claridge and Askew (1960, fig. 2), which is absent from the North American specimens identified as *E. tylodermatis*.

Pteromalidae

Three species of *Lyrcus* Walker, one species of *Mesopolobus* Westwood, one species of *Neocatolaccus* Ashmead, and what likely are two species of *Pteromalus* Swederus comprised about 96% of the reared parasitoids (Table 1).

Lyrcus is restricted to the New World. The genus is unrevised for the Nearctic, but Noyes (2002) listed 16 species from the region. Species identifications in this study are based on examination of type material of the North American species contained in the USNM, which excludes the four oldest names assigned to *Lyrcus* from the Nearctic. Walker (1847) described four species collected in Florida that are now classified in *Lyrcus* (Noyes 2002) and type material of these species is in The Natural History Museum, London. Although Burks (1975) examined the types, the names have yet to be placed adequately within a species concept of *Lyrcus*. Until this is done within a comprehensive taxonomic revision, it is possible that one or more of the four Walker names represents a senior synonym of a name used in this paper.

Lyrcus maculatus (Gahan) was the most commonly reared species of all the parasitoids, comprising 967 specimens (515 ♀♀, 452 ♂♂) or 86% of the parasitoid fauna. The distribution record is the first east of Illinois and Texas (Noyes 2002), but in western North America *L. maculatus* has often been reported as an incidental parasitoid of *C. obstrictus*. In the older literature it was identified as a species of *Trimeromicrus* Gahan or *Zatropis* Crawford. Gahan (1914) originally described *L. maculatus* as a parasitoid of the clover seed chalcid, *Bruchophagus platypterus* (Walker) (Hymenoptera: Eurytomidae). In addition to other species of *Bruchophagus*, it has also been reported as a parasitoid of the clover seed weevil, *Tychius picirostris* (Fabricius) (Yunus and Johansen 1967), the sunflower seed weevil, *Smicronyx fulvus* LeConte (Bigger 1933), the thistle seedhead weevil, *Rhinocyllus conicus* (Frölich) (Wilson and Andres 1986) (Coleoptera: Curculionidae) and, as a hyperparasitoid, of the alfalfa gall midge, *Asphondylia websteri* Felt (Diptera: Cecidomyiidae) (Gahan 1919). Among known species of *Lyrcus*, *L. maculatus* is usually distinguished by its distinctive mesoscutal colour pattern, as described in the key. Urbahns (1919, pl. 23A) provided a dorsal habitus of the female that illustrates this colour pattern. Included in the material we have identified as *L. maculatus* are about 25 unusually small, more or less brown specimens that either have quite obscure blue spots or that lack the spots entirely. The abnormally coloured individuals also have much finer, coriaceous mesonotal sculpture rather than the reticulate sculpture of typical specimens. However, some individuals are intermediate in both colour pattern and sculpture so that a very fine mesonotal sculpture and brown body colour without blue regions likely is correlated with small body size.

Lyrcus perdubius (Girault) was the second most commonly reared parasitoid, comprising 60 specimens (39 ♀♀, 21 ♂♂) or 5.3% of the parasitoid fauna. Georgia represents a new state distribution record for the species. Dosdall et al. (in press) first reared *L. perdubius* from canola seedpods in Alberta, putatively as a parasitoid of *C. obstrictus*, and Noyes (2002) listed *Anthonomus grandis*, *A. rutilus* (Boheman), *A. signatus* (Say), *Lixus musculus* Say, and *Smicronyx tychoides* Le Conte (Coleoptera: Curculionidae) as other hosts.

Six specimens (3 ♀♀, 3 ♂♂; 0.5% of the parasitoid fauna) of *Lyrcus incertus* (Ashmead) were also reared. This species is widespread throughout southern and eastern USA. Although *C. obstrictus* represents a new host association, Noyes (2002) listed several other genera and species of Curculionidae as hosts, including *A. grandis* and a single report of a *Ceutorhynchus* sp. (Pierce et al. 1912).

Only one female and male of *Mesopolobus moryoides* Gibson were reared, which rep-

resent 0.2% of the parasitoid fauna and the first distribution record for Georgia and eastern North America. This species is a common parasitoid of *C. obstrictus*, its only known host, in western USA (Gibson et al. 2005). Two other species of *Mesopolobus* have also been reported as putative parasites of *C. obstrictus* in western North America, *M. mayetiolae* (Gahan) in California (Carlson et al. 1951) and *M. bruchophagi* (Gahan) in Alberta (Dosdall et al. in press). *Mesopolobus moryoides* was misidentified as *Mesopolobus morys* (Walker) in North America until Gibson et al. (2005) correctly identified it and provided features to differentiate the two species from each other and from other regional species. *Mesopolobus* is yet another unrevised, speciose genus in North America, with Noyes (2002) listing 20 valid species for the region.

A total of 33 *Neocatolaccus tylodermae* (Ashmead) (13 ♀♀, 20 ♂♂) were reared, which represent 2.9% of the parasitoid fauna. Although Georgia is a new state distribution record, the species was known from Florida and is transcontinental in the USA (Noyes 2002). *Ceutorhynchus obstrictus* also represents a new putative host association, though Noyes (2002) listed 15 other curculionid species in 10 genera as hosts. Pierce (1909) reared it along with *E. cyaniceps* from *Lixus musculus*, Wilson and Andres (1986) reared it along with *L. maculatus* from *Rhinocyllus conicus*, and there is a single published association with *Anthonomus grandis* (Pierce 1909). Bouček (1993) provided a key to the three described North American species of *Neocatolaccus*. He differentiated *N. tylodermae* from *N. moneilemae* Gahan on the basis of a rounded rather than medially carinate pronotum and truncate rather than medially narrowly emarginate clypeus. Forewing setal differences also help to differentiate the species. In *N. tylodermae* the ventral surface of the costal cell has setae only over about its apical half and dorsally the forewing is bare behind about the basal half of the marginal vein so that three or four rows of ventral admarginal setae are visible within a distinct speculum (Fig. 43), whereas individuals of *N. moneilemae* have a line of setae along the length of the costal cell and the forewing is setose behind the marginal vein more or less to its base so that a distinct speculum is lacking and the admarginal setae are covered by dorsal setae.

Five individuals (2 ♀♀, 3 ♂♂; 0.5% of the parasitoid fauna) of *Pteromalus* were reared. One female was identified as *Pteromalus cerealellae* (Ashmead) based on examination of type material in the USNM, but the other specimens remain unidentified to species (see below). Girault (1917) provided a key to several species of *Pteromalus* (as *Habrocytus* Thomson) in North America, but there is no modern revision and Noyes (2002) listed 46 valid species names in the Nearctic region. In western North America, unidentified species of *Pteromalus* have been reported from surveys in Idaho (Walz 1957), Washington (Hanson et al. 1948), British Columbia (McLeod 1953), and Alberta (Dosdall et al. in press). Examination of voucher specimens from these studies by the senior author revealed at least one unidentified species common to the four areas as well as a single rearing of *Pteromalus puparum* (L.) from the surveys reported by McLeod (1953) in British Columbia (Gibson et al. 2006). The unidentified species from western North America and *P. cerealellae* belong to a comparatively small group of Nearctic species whose females have the line of setae on the ventral surface of the costal cell interrupted medially and the bare band behind the marginal vein extending the length of the vein (sometimes with one or two setae apically within an otherwise distinct bare band, Fig. 49). Females of the two species differ from each other most conspicuously in propodeal features. In *P. cerealellae* the setae on the callus extend mesal of the postspiracular sulcus posteriorly, almost to the

plical carina (Fig. 31), whereas females of the species from western North America have the region between the postspiracular sulcus and plical carina bare. The propodeal structure of *P. cerealellae* is very similar to that of the European species *Pteromalus semotus* (Walker) (Graham 1969, fig. 385), which was reported as reared from *C. obstrictus* in England and Poland (Murchie and Williams 1998). Bouček (1977) once considered the two names conspecific, but subsequently (Bouček 1988) re-established *P. cerealellae*. Among other features, *P. semotus* has an entire costal setal line (*cf.* Fig. 50). *Pteromalus cerealellae* was described from, and until recently was thought to be a monophagous parasitoid of, the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Noble 1932). Flanders (1932) stated that it would also oviposit into the tuberworm moth, *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae). However, Brower (1991) showed that it effectively parasitized 12 different species in 4 families of Coleoptera (including 3 species of Curculionidae) that are pests of stored products. He concluded that although the species probably prefers *S. cerealella*, it is more habitat specific than host specific.

The second *Pteromalus* female reared and that of *P. cerealellae* are similar in having the forewing dorsally bare behind the entire length of the marginal vein (Figs 49, 50), but differ in those features given in the key. A comprehensive generic revision is necessary to establish the correct species name of the unidentified female. The three unidentified males may represent the opposite sex of the unnamed female, based on the presence of a continuous line of setae on the costal cell, but species characteristics of male *Pteromalus* remain largely unknown and the males are not included in the key.

DISCUSSION

The parasitoid fauna reared from *B. napus* seedpods in Georgia, 1994 through 1996, revealed the same five chalcid families that have been reported as reared from *C. obstrictus* in western North America, including six species apparently shared in common (Table 1). Of the shared species, *L. maculatus* was by far the most commonly reared parasitoid in Georgia, comprising about 86% of the fauna. This contrasts to western North America where it appears to be only an incidental parasitoid of *C. obstrictus*. Furthermore, two common parasitoids of *C. obstrictus* in at least some parts of western North America, *N. tidius* and *M. moryoides*, were reared as only incidental parasitoids in Georgia. The latter rearings represent the first distribution records of the respective species in eastern North America. If *C. obstrictus* was introduced to Georgia from western North America, the two parasitoid species may have been introduced accidentally at the same time. The most common parasitoid of *C. obstrictus* throughout most of western North America, *T. lucidus*, was not reared in Georgia despite the statement of Buntin (1998) that most of the reared specimens consisted of *T. perfectus* (a misidentification of *T. lucidus* prior to Gibson et al. 2005). The second and third most commonly reared species in Georgia were *L. perdubius* and *N. tylodermae*, respectively. Because of their relative abundance and because neither has been reported from hosts other than Curculionidae (Noyes 2002), both species very likely are parasitoids of *C. obstrictus*. However, it remains to be determined whether they are primary or hyperparasitoids. At least some of the other incidental species, such as *C. torvina*, *B. allynii* and *E. cyaniceps*, likely are hyperparasitoids rather than primary parasitoids. The rearing of *E. glaucus*, *B. allynii*, *E. cyaniceps*, *L. incertus*, *P. cerealellae* and the unidentified species of *Pteromalus* from *B. napus* seedpods in Georgia represent new rearing records, but these are at most incidental parasitoids, if *C. obstrictus* was the actual host for all the species. Buntin (1998) obtained the parasitoids from mass-reared seedpods. The

very few *Asaphes* and *Pachyneuron* that were reared, along with several Aphidiinae (Braconidae) also preserved with the material, show that some aphid mummies contaminated the seedpods even though an attempt was made to remove these prior to rearing. Likewise, one or more of the uncommon parasitoid taxa may have emerged from other undetected insects within or on the pods. For example, the only other host record for *E. glaucus* is a lepidopteran. Individual rearing of parasitoids dissected from seedpods is necessary to definitively prove the host associations listed in Table 1, which at present are only inferred.

Both *L. incertus* and *L. perdubius* have been reported previously as parasitoids of the cotton boll weevil, as has also *E. cyaniceps*, *E. tylodermatis*, and *N. tylodermae*, though not the most commonly reared parasitoid of *C. obstrictus* in Georgia, *L. maculatus*. These results suggest that the chalcid parasitoid fauna acquired by *C. obstrictus* in any area where it is introduced is partly influenced by what other curculionid species occur in the region. If so, the parasitoid fauna from eastern Canada and the southeastern USA might be expected to differ as substantially as between eastern and western North America.

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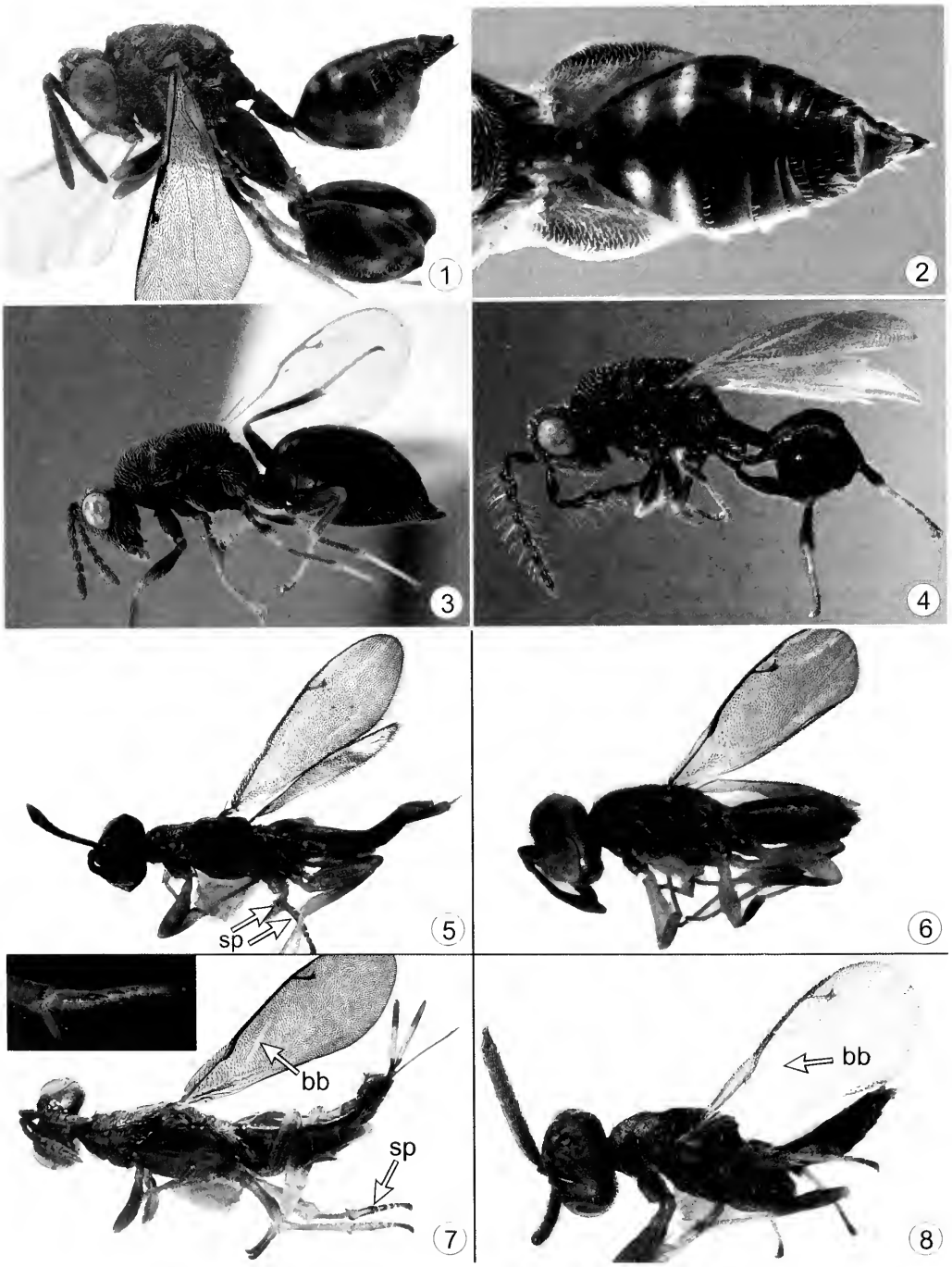
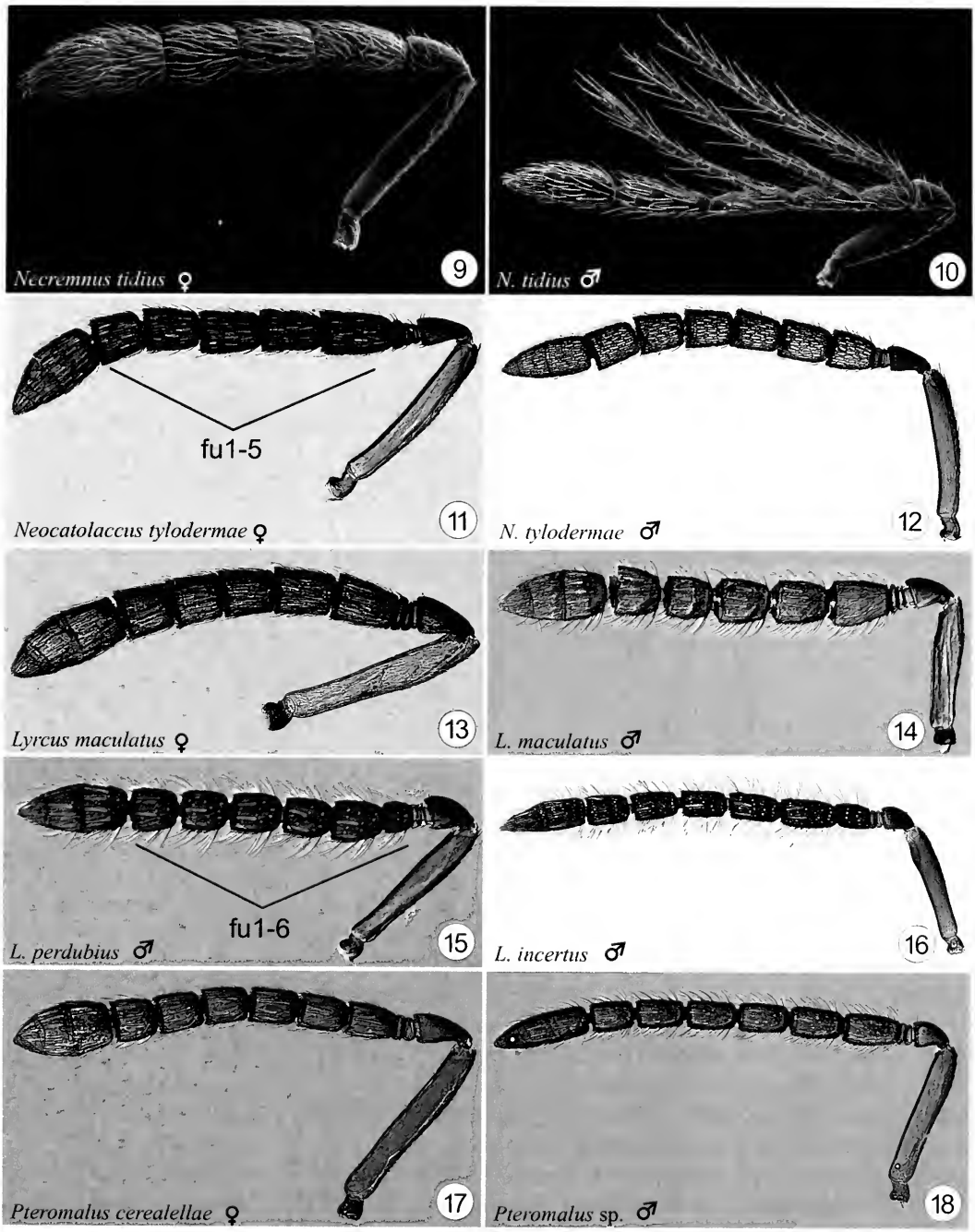
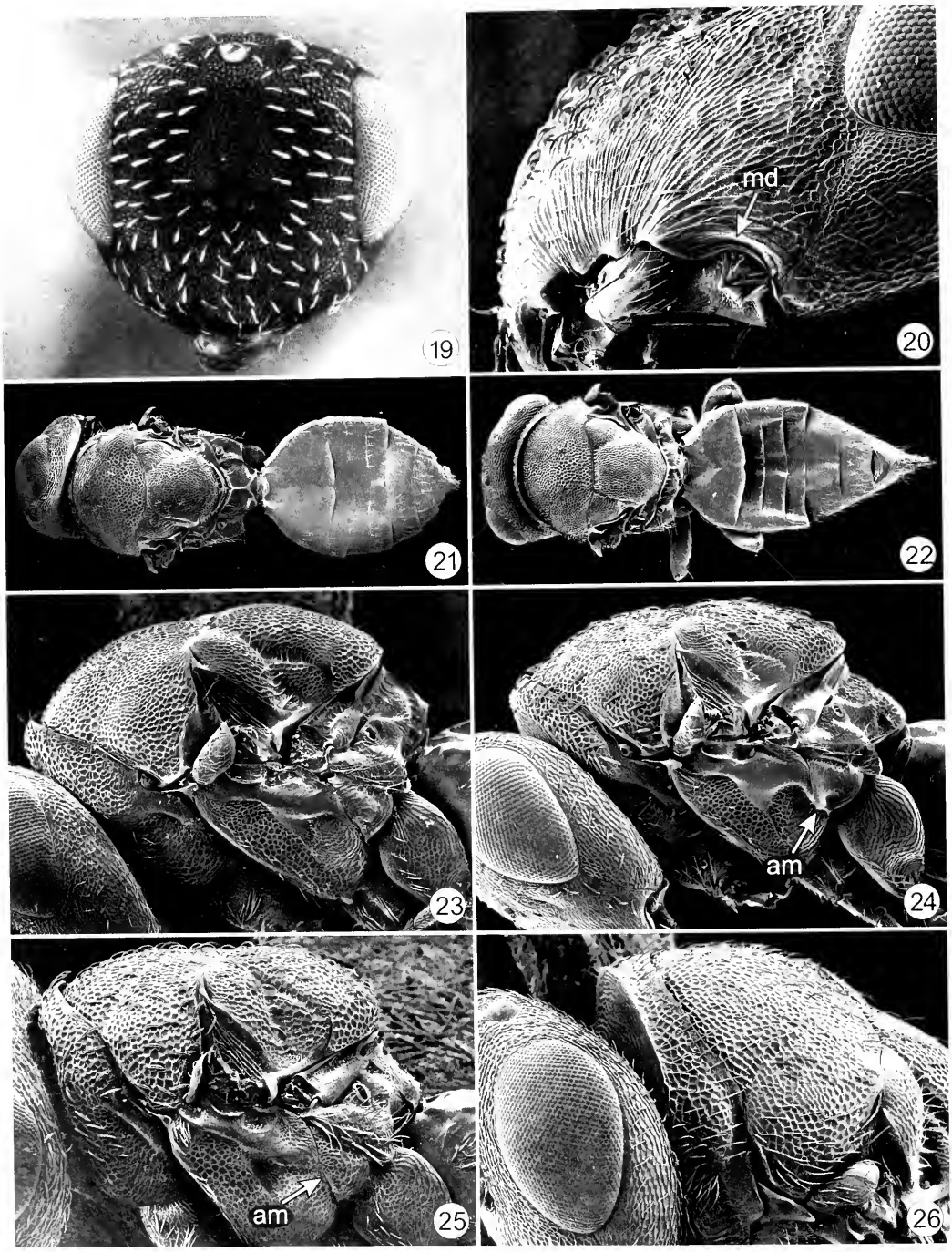


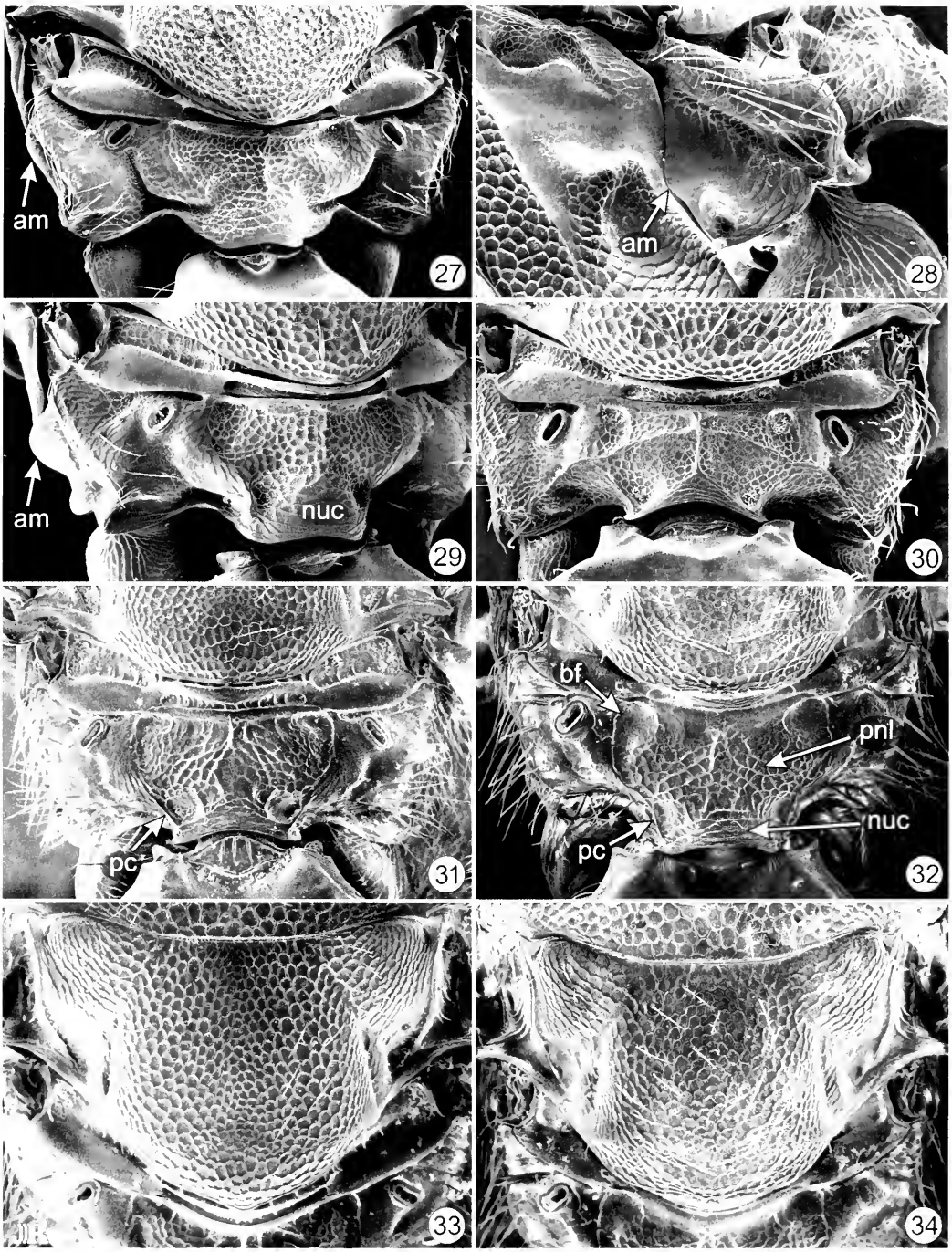
Figs 1–8. 1 and 2, *Conura torvina*, female: 1, lateral habitus; 2, metasoma, dorsal. 3 and 4, *Eurytoma tylodermatis*, lateral habitus: 3, female; 4, male. 5 and 6, *Brasema allynii*, lateral habitus: 5, female; 6, male. 7 and 8, *Eupelmus cyaniceps*, lateral habitus: 7, female (insert: mesotarsus and apex of mesotibia showing spines); 8, male. (Abbreviations: bb = bare band, sp = spines.)



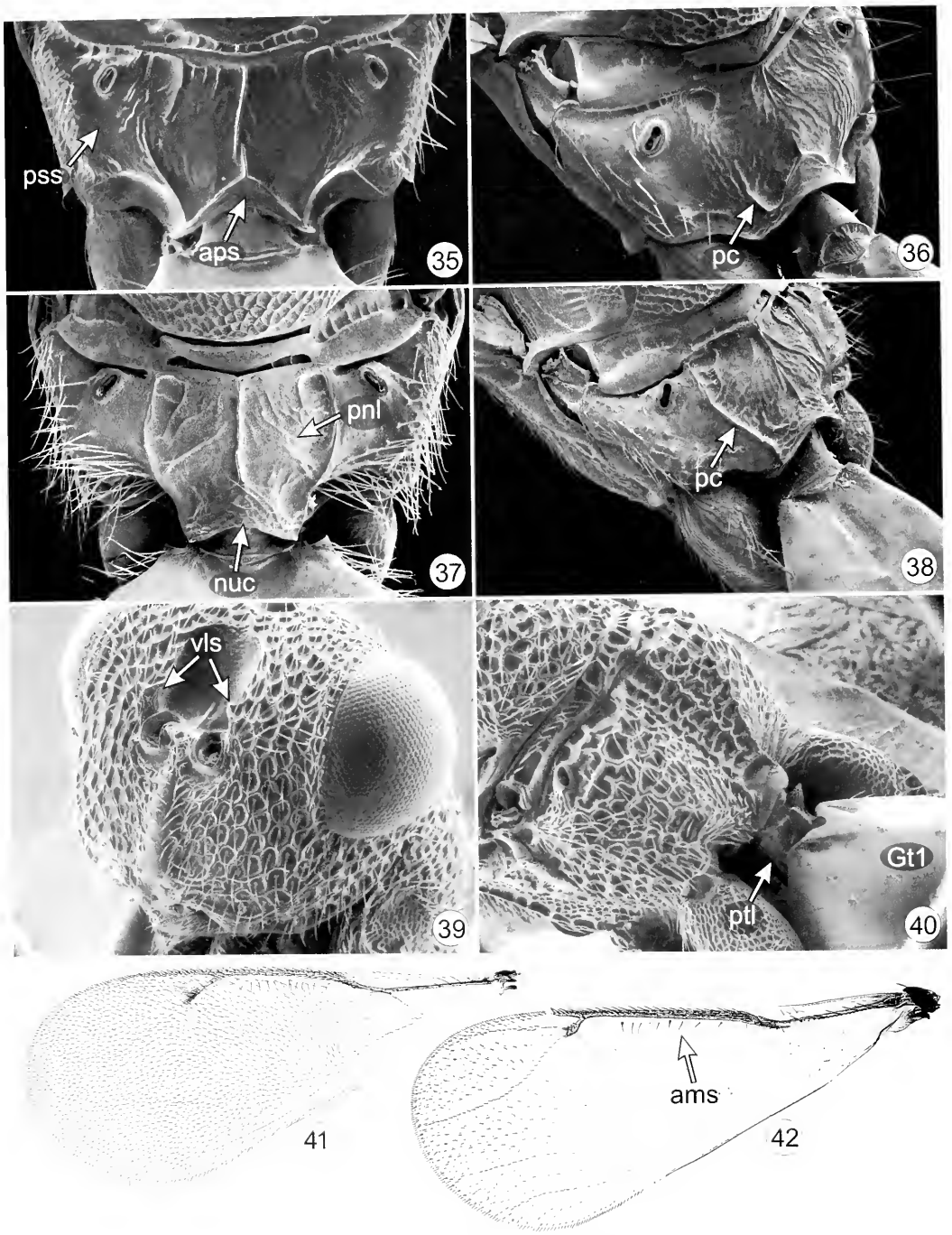
Figs 9–18. Antenna, male and female. (Abbreviations: fu = funicular segment.)



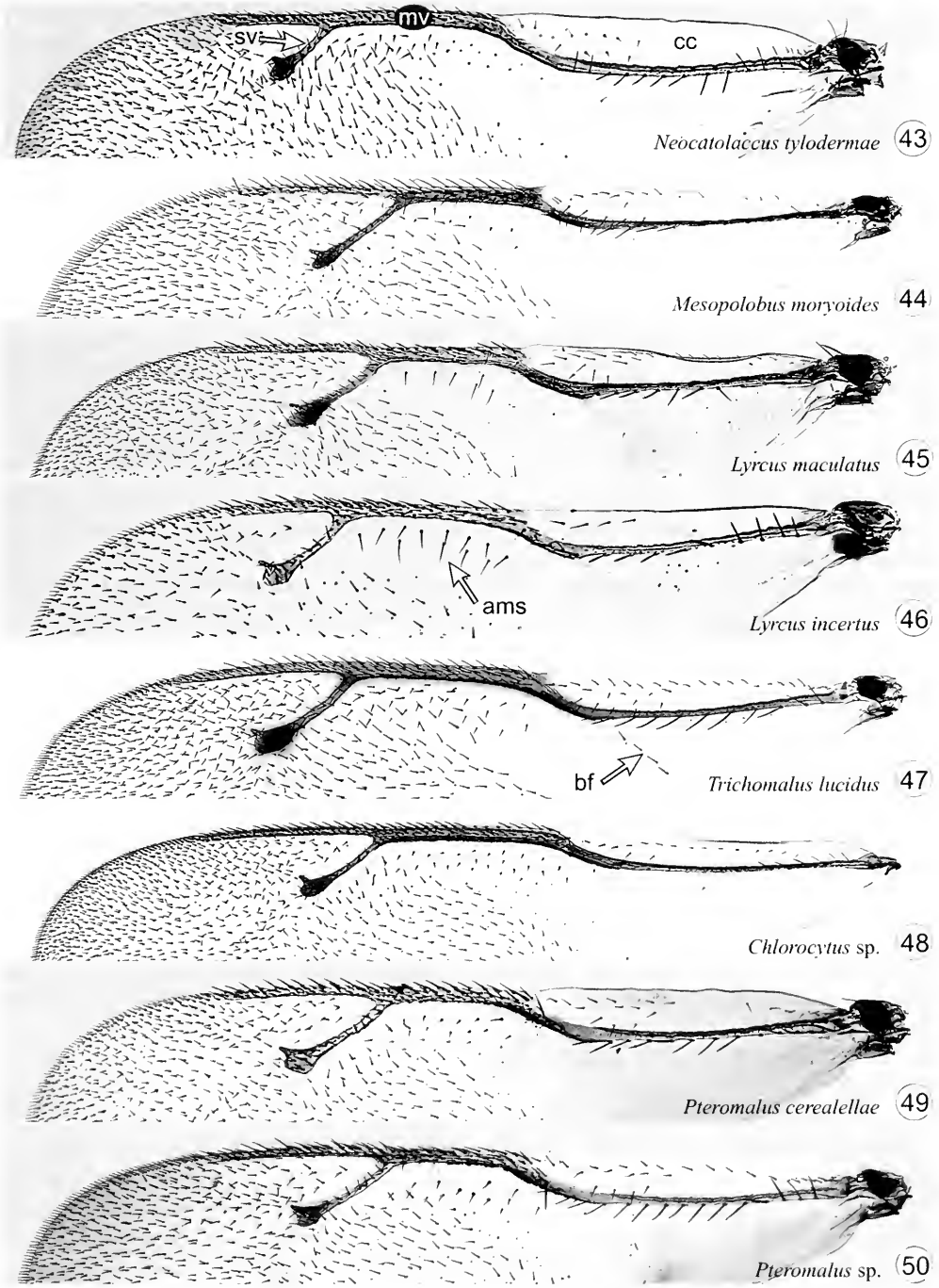
Figs. 19–26. 19, *Lyrcus perdubius*, head. 20, *L. incertus*, malar space. 21 and 22, dorsal habitus, female: 21, *Mesopodobus moryoides*, 22, *L. maculatus*. 23–25, mesosoma, lateral: 23, *L. maculatus*; 24, *L. perdubius*; 25, *Neocatolaccus tylodermae*. 26, *Trichomalus perfectus*, pronotum and mesoscutum. (Abbreviations: am = anterior margin of metapleuron, md = malar depression.)



Figs 27–34. 27 and 28, *Lyrcus incertus*: 27, propodeum; 28, metapleuron. 29–32, propodeum: 29, *L. perdubius*; 30, *Neocatolaccus tylodermae*; 31, *Pteromalus cerealellae*; 32, *Pteromalus* sp. 33 and 34, scutellar-axillar complex: 33, *P. cerealellae*; 34, *Pteromalus* sp. (Abbreviations: am = anterior margin of metapleuron, bf = basal fovea, nuc nucha, pc = plical carina, pnl = propodeal panel.)



Figs. 35–42. 35 and 36, *Chlorocytus* sp., propodeum: 35, female, posterior; 36 male; posterolateral. 37 and 38, *Trichomalus lucidus*, propodeum: 37, female, posterior; 38, male, posterolateral. 39 and 40, *Eurytoma tylodermatis* female: 39, head, frontolateral; 40, propodeum and base of metasoma, dorsolateral. 41 and 42, forewing: 41, *Necremnus tidius*; 42, *Euderus glaucus*. (Abbreviations: ams = admarginal setae, aps = adpetiolar strip, Gt1 = first gastral tergite, nuc = nucha, pc = plical carina, pnl = propodeal panel, pss = postspiracular sulcus, ptl = petiole, vls = ventrolateral margin of scrobes.)



Figs 43–50. Forewing, female. (Abbreviations: ams = admarginal setae, bf = basal fold, cc = costal cell, mv = marginal vein, sv = stigmal vein.)

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A Survey of the Bees of the Black Rock Forest Preserve, New York (Hymenoptera: Apoidea)

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Abstract.—We present the results of a survey of the bee fauna of Black Rock Forest, Orange County, New York, USA. The survey focused on bees, with more limited data gathered for other incidentally collected groups such as apoid and vespid wasps. Surveys in 2003 with nets and bowls recorded 144 bee species (26 genera), 22 vespid species (9 genera) and 23 crabronid species (12 genera). Noteworthy records are detailed. A preliminary checklist of the bee fauna of the BRF is presented and discussed in relation to that of New York State, selected sites within the state, and of the northeastern USA as a whole. The cleptoparasitic species *Sphecodes fattigi* Mitchell, *Sphecodes johnsonii* Lovell, and *Lasioglossum* (*Dialictus*) *michiganense* (Mitchell), and the oligolectic species *Osmia* (*Melanosmia*) *inermis* (Zetterstedt) are newly recorded from New York State. Ecological patterns pertaining to sociality, nest type, pollen specialization, parasitism, and phenology, are summarized and discussed, as are the efficacies of different collecting methods. The net collected sample was richer than the bowl trapped sample in total bee species (117 vs. 113) and in the number of unique species (29, 20.4% vs. 25, 17.6%).

Key words.—native bees, *Bombus*, *Andrena*, Apidae, invertebrate survey, invertebrate biodiversity, bowl trap, pan trap, trap nest, Black Rock Forest, pollination

Bees (Hymenoptera: Apoidea) are the single most important animal pollinators of both native and cultivated vegetation in most habitats worldwide (Williams et al. 2001, Michener 2000). The mutualist relationship between bees and plants forms a key process in the maintenance of both local biological diversity and agricultural productivity. As primary pollinators, bees provide a vital ecosystem service, affecting the integrity of ecological communities as a whole, including the health of humans (Williams et al. 2001, Nilsson 2000, Cane and Tepedino 2001). Despite this ecological importance, our understanding of some basic aspects of bee biology, including species level distributional patterns, remains incomplete. There are about 20,000 species of bees worldwide (Michener 2000) and approximately 3500 described species occur in America north of Mexico (JSA and T. Griswold, unpublished; cf. Hurd 1979). Published data on the distribution of bees in New York State (NY) is limited (e.g., Leonard 1928), but Ascher (unpublished information) has compiled a list of 423 species known from New York, of which 405 are native to North America.

Single-site inventories of poorly known invertebrate groups have the potential to establish useful quantitative baseline estimates of local biodiversity, as well as to help illuminate large-scale distributional patterns within those groups. Such estimates can prove useful in testing hypotheses arising from practices as diverse as theoretical biogeography and conservation planning. In addition, geo-referenced specimen data are amenable to re-analysis and comparison with related data sets in the context of regional studies of biodiversity across diverse groups. Finally, such in-

ventories help to address the need for natural history information that is crucial for understanding community-level ecological patterns (e.g. phenological patterns, host associations, habitat use, etc).

Black Rock Forest (BRF) harbors a variety of distinct habitat types, many of which are typical of the larger Hudson Valley Region, and is managed in part as a long-term research preserve. Because the landscape matrix surrounding BRF is under increasing pressure from land conversion and habitat degradation, a survey of the bee communities of BRF while surrounding habitats are still relatively intact should provide a valuable basis for future comparison with a variety of other sites across a range of spatial and temporal scales. The effects of environmental change on bee communities remain insufficiently understood. Many relevant studies have been published (see, e.g., Matheson et al. 1996), but few of these are from eastern North America. Cane (2005) notes that bees "possess a unique combination of salient foraging and nesting traits that together set them apart from other taxa studied in the context of habitat fragmentation". Many bees utilize open areas for foraging and nesting, and may benefit from forest fragmentation, unlike forest-dwelling songbirds. However, bees are still potentially vulnerable to habitat change, particularly the loss of their host plants.

RESEARCH OBJECTIVES

This survey was undertaken with two primary goals; first, to assemble a faunal list of the bees (and selected aculeate wasps) of BRF to serve as a baseline inventory of use to both ecologists and conservation biologists, and second, to compare BRF data with other bee samples in order to shed light on larger-scale (regional) patterns of bee distributions and diversity. Second order objectives included enhanced representation of the regional bee fauna in the collection of the American Museum of Natural History (AMNH) and creation of a synoptic (taxonomic reference) collection to be housed at BRF. Ecological data were also gathered, such as abundance of bees across the season and on selected host plants, and the efficacies of various collecting methods (net collecting vs. trapping with bowls of three different colors vs. trap nesting) were tested.

STUDY SITE AND METHODS

The Black Rock Forest (BRF) is a 1520 hectare preserve and research facility located in Orange County, New York (Lat. 41.42267, Long. 74.03039), ca. 50 miles north of New York City (NYC). The BRF is situated within the highest portion of the Hudson Highlands. The terrain comprising the preserve ranges in elevation from about 135 m to 446 m. A network of closed canopy dirt roads permits access to within 1 kilometer of any point within the BRF. The landscape, both within the forest preserve, and across several large adjacent tracts (including West Point Military Academy), is mostly forested (upland hardwood forests dominated by *Quercus* spp., Barringer and Clemants 2003). Other local habitat types include successional hardwood stands, hemlock coves, chestnut-oak woods, red maple swamps, ponds, reservoirs, and marshes. Important habitats for bees at BRF include small meadows, exposed road edges and reservoir edges, dams, and marshes, where flowering shrubs (such as *Viburnum* spp., *Ilex verticillata* (L.) A. Gray, *Kalmia latifolia* L., *Clethra alnifolia L.*, *Spiraea* spp., *Rhododendron* spp.), and herbs (such as *Veronica*, *Polygonum* spp., *Gnaphalium*, *Solidago* spp., and *Viola* spp.) provide seasonal sources of pollen and nectar to bees. In addition, during early spring (April) prior to leafout, forest habitats hosted bees attracted to flowering trees such as *Acer rubrum* L., *Salix* spp. including *S. discolor* Muhl. and *Prunus* spp. In May, other flowering trees such as *Crataegus macrosperma* Ashe. and other *Prunus* spp. were important re-

sources for many *Andrena* and other bee species. The early spring flower *Erythronium americanum* Ker-Gawler flowered sparingly during our survey season and was visited by relatively few bees. *Vaccinium* species, especially highbush blueberry *Vaccinium corymbosum* L. and lowbush blueberry *V. angustifloium* Ait. dominated large areas of the forest understory at BRF, including dry hillsides, damp forest areas, open forest gaps created by fires, and wet marsh edges in association with herbaceous communities. Beginning in May, and continuing into late June, *Vaccinium* stands composed of several species were visited by large concentrations of nectaring and "buzz" pollen-collecting bees. *Vaccinum stamineum* L. (Deerberry) was moderately common in hillside forests. Patches of *Lysimachia* were noted.

The survey season during the spring and summer of 2003 was generally wet and cool in southern New York as confirmed by weather data collected at BRF. Above average rainfall and below average temperatures would be expected to depress bee numbers and collecting success.

Sampling schedule.—We conducted bee surveys at BRF during 24 days between 31 March 2003 and 16 October 2003. Each survey day began at approximately 0730 hr and was completed generally between 1800 hr and 1900 hr. Most fieldwork was conducted on days with predominantly sunny skies and warm temperatures. Collection sites visited per sampling day and the time spent at each site varied. In addition, individual collecting sites were chosen throughout the BRF property opportunistically in response to the presence of bees or abundance of flowering plants. UTM coordinates were recorded for all sites where bees were collected.

Sampling methods.—We collected bees at BRF using 3 principal methods: colored plastic pan (or bowl) traps, hand-held insect nets, and wooden trap nests. Bowl traps were made from 6 oz. plastic Solo brand bowls that were spray-painted with one of three florescent colors: yellow, white or blue. A total of 150 traps were deployed on each of 17 survey visits and arrayed in ten transects on each visit. Each transect consisted of 15 traps (five of each color), arrayed in alternating colors. Traps contained a solution of Dawn brand blue dishwashing liquid (1 table spoon to 1 gallon tap water) and were placed in ten sites on the ground along transect lines. Traps were deployed over a period of approximately 1 hour beginning at 0730 hr and were in place before 0900 hr on survey visits during which they were used. Individual traps were placed at approximately one meter apart. Transect sites were chosen opportunistically and included: open fields, roadsides, reservoir edges, dams, forest floors and stone outcroppings throughout the BRF property. At the close of each survey visit the traps were retrieved during a two-hour period beginning at approx. 1600 hr. The contents were poured through sieves and the recovered specimens were transferred to plastic whirl-packs containing 75% ethyl alcohol. Locality data and bowl trap color labels were recorded.

Hand netting of bees was conducted between 09:00 and 16:00 during 23 survey visits. Collecting by hand-net was undertaken opportunistically at sites where bees were thought to be concentrated. Hand netting was pursued most intensively in exposed sunny habitats such as fields, road edges, reservoir and marsh edges, where many shrubs and herbaceous perennials bloom and where bees were most likely to occur. When bees were captured they were transferred to cyanide killing jars before being stored in vials. Vials were labeled and placed in a cooler for transfer to the laboratory.

Twenty wooden 'Binderboard' brand trap-nests were deployed for the duration of the survey beginning on 27 May 2003. Ten trap-nests consisted of a wooden block bearing 39 holes, each measuring 5.5 mm diameter, and a depth of 10 cm. The

remaining 10 trap-nests were similar in other respects, but each bore 21 holes measuring 5 mm in diameter, drilled to a depth of 16 cm. Each hole was lined with a kraft paper tube to facilitate recovery of specimens. Trap-nests were mounted in sets of two, at 10 sites dispersed across the BRF property. Each nest was hung from a tree limb approximately 1.5 meters above the ground with the holes oriented to face south. Trap nests were checked periodically to determine if any Hymenoptera had inhabited the holes and to ensure that they were intact and undisturbed. Trap nests were retrieved from BRF on 20 March 2004, and each trap-nest was examined in the laboratory for evidence of occupation by Hymenoptera.

Specimens were sorted, mounted, and identified to species by the authors (initially sorted by VG; species determinations then made or confirmed by JSA) except the more difficult metallic *Lasioglossum* (*Dialictus*) females, determined by S. Droege, Vespidae, determined by J. M. Carpenter, and the more difficult Crabronidae, determined by P. Gambino. S. Droege made, confirmed, and revised identifications for numerous *Nomada*, and L. Day made and confirmed identifications of *Bombus sandersoni* and *B. vagans*. Vouchers are deposited in the collection of the American Museum of Natural History (AMNH). A synoptic collection is housed at the BRF research facility. Duplicate specimens were dispersed to various bee specialists.

Comparative data on the North American bee fauna as a whole, and on the fauna of New York State (NY), and of particular areas within NY, were compiled by JSA based on study of relevant taxonomic and faunistic literature and study of historical insect collections, especially those housed at: AMNH; Cornell University (CUIC); New York State Museum; National Museum of Natural History; University of Connecticut Insect Collections, Storrs; and Parker Gambino's personal collection (affiliated with the AMNH). Recent collections from across NY and from nearby states such as Connecticut were available, including material collected by the authors, P. Gambino, S. W. T. Batra, K. N. Magnacca, B. N. Danforth, D. L. Wagner, R. G. Goelet and their associates. All discussion of the past and present status and life histories of bee species found at BRF is based, in part, on these historical and recent collections and the literature in addition to the sample obtained during the survey of BRF. Totals cited for "southern New York" are for the area encompassing New York City (NYC), Long Island, and all counties adjacent to Orange County (i.e. the southeast portion of the state north to Sullivan, Ulster, and Dutchess Counties).

RESULTS AND DISCUSSION

The survey collected and individually databased 6,542 bee specimens representing 144 species, of which 138 are native and six are exotic (Appendix 1), 26 genera, and five families (Table 1). Of these, several records detailed below represent notable range extensions, the only recent known collection of a species in NY, or otherwise fill gaps in the known distributions of New York State bees. Other aculeate specimens incidentally sampled included 22 vespid species (9 genera), 24 crabronid species (13 genera), and 2 species of *Isodontia* (Sphecidae *sensu stricto*) (Appendix 2). Only a single bee, an *Osmia cornifrons* female, emerged from our trap nests. These were occupied primarily by eumenine (Vespidae) and *Trypoxylon* (*Trypoxylon*) (Crabronidae) wasps and were not examined in detail due to the lack of bees.

Species totals.—Of the 144 bee species found at BRF we regard 138 as native to North America (Appendix 1). These are discussed first followed by the six species known or suspected to have been introduced deliberately or accidentally to North America from Europe or East Asia.

Native bee species.—

Table 1. Summary of the number of described bee species for each genus known from New York State, with totals for the Eastern USA (sensu Mitchell 1960, 1962), New York State (NY), southern NY as defined in the text (SNY), Black Rock Forest (BRF), New York City (NYC; i.e. the five boroughs), and Ithaca (within city limits; many additional species are known from the Ithaca vicinity in Tompkins Co.). The number of species not native to North America (i.e. adventive and introduced species) is given in parentheses following the total number of species. *No recent records.

Superfamily Apoidea: Clade Anthophila (Bees)	EUSA	NYS	SNY	BRF	NYC	Ithaca
Family Colletidae:						
Subfamily Colletinae						
Colletes	35	17	7	2	7	6
Subfamily Hylaeinae: Tribe Hylaeini						
Hylaeus	24(3)	14(2)	8(2)	2	8(3)	10(2)
Family Halictidae						
Subfamily Rophitinae: Tribe Rophitini						
Dufourea	3	1	1	0	0	0
Subfamily Halictinae						
Tribe Augochlorini						
Augochlorella	3	1	1	1	1	1
Augochlora	1	1	1	1	1	1
Augochloropsis	3	1	1	1	1	1
Tribe Caenohalictini						
Agapostemon	4	4	4	2	3	3
Tribe Halictini						
Subtribe Sphecodina						
Sphecodes	34	25	15	4	8	13
Subtribe Halictina						
Halictus	5	4	3	3	3	3
Lasioglossum	114(2)	67(2)	39(1)	29(1)	25(1)	44(2)
Family Andrenidae						
Subfamily Andreninae: Tribe Andrenini						
Andrena	125(1)	87(1)	70(1)	40(1)	58(1)	66(1)
Subfamily Panurginae						
Tribe Calliopsini						
Calliopsis	3	1	1	1	1	1
Tribe Protandrenini						
Pseudopanurgus	15	4	2	1	1	1
Tribe Panurgini						
Subtribe Panurginina						
Panurginus	3	1	0	0	0	0
Subtribe Perditina						
Perdita	27	7	1	0	3	2
Family Melittidae						
Subfamily Melittinae						
Tribe Macropidini						
Macropis	4	3	3	0	3*	2
Tribe Melittini						
Melitta	3	1	1	0	0	1
Family Megachilidae						
Subfamily Megachilinae						
Tribe Anthidiini						
Anthidiellum	2	1	1	0	0	1
Anthidium	4(2)	2(2)	2(2)	1(1)	2(2)	2(2)
Paranthidium	1	1	1	0	0	1

Table 1. Continued.

Superfamily Apoidea: Clade Anthophila (Bees)	EUSA	NYS	SNY	BRF	NYC	Ithaca
Stelis	15	6	2	2	1	4
Tribe Osmiini						
Chelostoma	3(2)	3(2)	2(1)	0	1	3(2)
Heriades	3	3	1	1	2	1
Hoplitis	8(1)	6(1)	3	2	1	4
Osmia	30(4)	20(3)	12(3)	10(2)	5(3)	13(2)
Tribe Megachilini						
Megachile	43(5)	22(4)	17(2)	7(2)	16(4)	13(2)
Coelioxys	25	12	7	2	5	9
Family Apidae						
Subfamily Xylocopinae						
Tribe Xylocopini						
Xylocopa	2	1	1	1	1	1
Tribe Ceratinini						
Ceratina	4	3	3	2	3	3
Subfamily Nomadinae						
Tribe Nomadini						
Nomada	76	47	25	18	19	26
Tribe Ammobatoidini						
Holcopasites	3	2	1	0	0	2
Tribe Epeolini						
Epeolus	21	7	4	0	1	3
Triepeolus	26	7	1	0	1	2
Subfamily Apinae						
Tribe Osirini						
Epeoloides	1	1*	1*	0	1*	0
Tribe Emphorini						
Ptilothrix	1	1	0	0	1	0
Tribe Eucerini						
Eucera	7	1	1	0	0	0
Melissodes	27	12	6	2	9	8
Peponapis	1	1	1	0	1	1
Svastra	5	1	0	0	1*	0
Tribe Anthophorini						
Anthophora	6(1)	4	3	1	3	3
Habropoda	1	1	0	0	0	0
Tribe Bombini						
Bombus	21	18	15	8	12	15
Tribe Apini						
Apis	1(1)	1(1)	1(1)	1(1)	1(1)	1(1)
TOTALS:	743(22)	423(18)	269(13)	144(8)	210(15)	274(15)

Colletidae

We collected only two species of *Colletes*, *C. compactus* and *C. simulans*, neither of which was numerous. This scarcity of individuals and species (vs. the nine known from southern NY; see Table 1) may reflect the low frequency with which *Colletes* is captured in bowls (S. Droege, T. Griswold, pers. comm.) and perhaps a scarcity of appropriate sandy nest banks in the vicinity of the sampling sites. Absence of *Colletes inaequalis* Say in net-collected samples from early spring is surprising, as this is a conspicuous and locally abundant species across much of the northeastern USA and is often encountered as it collects pollen from maples (*Acer* spp.), which are numerous at BRF.

Our sample of *Hylaeus*, including small series of only two ubiquitous *Hylaeus* spp., *H. mesillae* and *H. modestus*, is also impoverished. At least four additional species are abundant in nearby Putnam County (JSA and P. Gambino, unpublished) and should occur at BRF.

Halictidae

All three augochlorine species known from NY are numerous at BRF. The abundance of *Augochlora pura* in our samples probably reflects the local availability of rotting logs in which this species excavates its nests. The most abundant bee in our sample, *Augochlorella aurata* (1,222 individuals collected) is a eusocial, ground-nesting species that is numerous across most of eastern North America. Populations of this species from northeastern USA and southern Canada were known as *A. striata* (Provancher) prior to recent synonymy with *A. aurata* in Coelho's (2004) revision of *Augochlorella*.

The two most common species of *Agapostemon* in NY (*A. sericeus* and *A. virescens*) were collected, but two species present more locally in southern NY [*A. texanus* Cresson and *A. splendens* (Lepeletier)] were not found. Absence of *A. splendens* is not surprising, as this species seems to be associated with sandy nesting substrates.

The cleptoparasitic genus *Sphecodes* was represented by *S. galerus*, *S. levis*, *S. fattigi*, and *S. johnsonii*, the last two recorded for the first time in NY (JSA has also collected *S. johnsonii* in Fairfield County, Connecticut, new state record). Two additional *Sphecodes* species, *S. atlantis* Mitchell and *S. dichrous* Smith, not found at BRF were collected elsewhere in Orange County in 1962 (Tuxedo Park vicinity; AMNH).

Three *Halictus* species ubiquitous in the eastern United States were found in good numbers, but the more precinctive *H. parallelus* Say was not collected.

Lasioglossum sensu stricto was represented by *L. coriaceum* and *L. leucozonium* (regarded for the first time as exotic, see below), both widely distributed across NY, and by two species, *L. acuminatum* and *L. fuscipenne*, restricted to eastern NY (e.g., absent from the Fingerlakes Region; see range maps in McGinley 1986).

Two widely distributed, pollen-generalist species of carinate *Lasioglossum* (*Evylaeus*) (sensu Michener 2000) were collected (*L. cinctipes* and *L. quebecense*) in addition to the more localized *L.* (*Evylaeus*) *nelumbonis*. The latter seems to be strongly associated with aquatic emergent flowers. In our study, numerous *L. nelumbonis* were collected in pan traps placed along a causeway bisecting Jim's Pond, in which grew abundant Nymphaeaceae (*Nymphaea odorata*). Museum label data suggest that *L. nelumbonis* may be a pollen-specialist of Nymphaeaceae and/or Nelumbonaceae, but direct observations of pollen collecting behavior by this species have not yet been made due to the difficulty of observing and collecting bees on aquatic vegetation.

Lasioglossum (*Dialictus*) individuals were, as expected, particularly abundant in our bowl samples. These were found to belong to 22 identified species (additional, poorly known species may be included among our undetermined metallic *Dialictus*; most males of this subgenus were not determined) including two socially parasitic species (*Paralictus* sensu Mitchell 1960) and two black, non-metallic *Dialictus* species (=noncarinate *Evylaeus*; see Michener 2000). Among the identified species of metallic, pollen-collecting *Dialictus* collected in BRF (i.e., *Dialictus* sensu Mitchell 1960) the wood-nesting species *L. coeruleum*, *L. cressonii*, and *L. oblongum* were each numerous. Other notable metallic, pollen-collecting *Dialictus* species include two species typical of northern forests (*L. nigroviride* and *L. versans*), a distinctive species often found in sand pits (*L. heterognathum*), and an infrequently recorded species (due in part to identification difficulties) previously known in NY from a few specimens collected in or near the lower Hudson River Valley (*L. cattellae*). Single

females of the two socially parasitic *Dialictus* species were collected, one of which, *L. michiganense*, has previously been recorded in the literature solely from Mitchell's (1960) unique holotype female, collected in Wayne County, Michigan, in 1940. Our single female specimen and another female collected 30 June 2004 at the inlet to Lake Myosotis, Edmund Niles Huyck Preserve, Rensslaerville, Albany County, NY, by JSA and C. J. Daley are the first records outside of Michigan. Despite a lack of published records, this species is probably widely distributed across the northeastern USA. It was recently found in Maryland (S. Droege, pers. comm.; new state record) and southern Ontario, Canada (L. Packer, pers. comm; new Canadian record). The male of this species remains unknown. The female of *L. michiganense* possesses a conspicuous, inner, subapical mandibular tooth, whereas the mandibles of other parasitic female *L.* (*Dialictus*) are simple (i.e., lack an inner tooth) with elongate slender tips. The other socially parasitic *Dialictus* found at BRF, *L. cephalotes*, has recently been found in NYC in Central Park, Prospect Park (JSA, new records), and the Bronx (collected by P. Gambino).

Andrenidae

Our BRF sample included 40 species of *Andrena* but is still far from complete, as an additional 32 species known from southern NY were not recorded. Our sample was rich in vernal species characteristic of northeastern forests such as *A. imitatrix* and *A. nivalis*. Species associated with blueberry were particularly well represented including the *Vaccinium* oligoleges (pollen specialists) *A. bradleyi* and *A. carolina*, and the polylectic *A. carlini* and *A. rufosignata*. The last species is abundant (but under-collected; cf. LaBerge 1980) in northern blueberry bogs, and evidently reaches the southern limits of its range at or near Black Rock Forest, as it is unknown from New York City, Long Island, and elsewhere along the mid-Atlantic coast. The long malar space of *A. rufosignata*, in comparison to its likely sister species *Andrena mandibularis* (LaBerge 1980), may be an adaptation to collecting nectar from the bell-shaped corollas of *Vaccinium* species. Another oligolectic *Andrena* collected, *A. cornelli*, is now thought to be a *Rhododendron* specialist based on field observations by JSA in Virginia, label data for newly identified material in museum collections, and the widely spaced scopal hairs of this species that can be considered an adaptation that holds *Rhododendron* pollen connected by viscin threads (Ascher, unpublished; cf. LaBerge 1980). *Andrena violae*, an oligolege of *Viola*, possesses elongate maxillary palpi used to extract nectar from its host. *Viola* is otherwise most often visited by long-tongued bees such as *Osmia* that are able to reach its concealed nectaries. *Andrena violae* is numerous across much of the eastern United States, excluding the colder areas of the northeast, but was previously known in NY solely from a single male collected at Van Natta's Dam, Six Mile Creek, Ithaca, Tompkins County, 2 May 1936 (specimen examined, CUIC). This species was not represented among collections made on *Viola* at this site and elsewhere in the Fingerlakes Region by JSA during 1997–2002, so evidence of its persistence in NY at a new station of occurrence is welcome. Other oligolectic *Andrena* at BRF include *A. krigiana*, a specialist of *Krigia* (dwarf dandelion), and *A. fragilis*, a specialist of *Cornus* (*Svida*). Three *Andrena* specialists of *Solidago* and *Aster* (tribe Astereae) were found, *A. hirticincta*, *A. nubecula*, and *A. simplex* (but not its sister species, *A. placata* Mitchell, which has been collected recently in Putnam Co., NY), as was the panurgine Astereae specialist *Pseudopanurgus andrenoides* [we recognize genus *Pseudopanurgus* in the broad sense of Mitchell, 1960, including *Protandrena* (*Heterosarus*) and *P.* (*Pterosarus*) of Michener, 2000]. *Andrena arabis* is a specialist of Brassicaceae that may actually benefit from spread of in-

vasive Garlic Mustard *Alliaria petiolata* (Bieb.) Cavara & Grande. Many species that regularly collect pollen from rosaceous trees and shrubs, and are known or suspected to be important pollinators of apples, were collected in good numbers, including *A. miserabilis*, *A.* (*Melandrena*) spp., and *A.* (*Trachandrena*) species. *Andrena* (*Trachandrena*) *nuda* was numerous at BRF, which is near the northern edge of its range in NY (see map in LaBerge 1973).

Melittidae

Although a deliberate effort was expended to locate and collect from *Vaccinium stamineum*, the host plant of *Melitta eickworti* Snelling and Stage (1995), this recently described species was not recorded during our survey. However, it has been collected nearby in Putnam County by P. Gambino, as has *O. virga* Sandhouse, another poorly known oligolege of Ericaceae (see Cane et al. 1985; they recorded *O. virga*, as *O. "felti"*, collecting "surprisingly pure" loads of Deerberry pollen; this species also uses other ericaceous hosts, M. Arduser pers. comm.). No *Macropis* were collected in this study although their host plant *Lysimachia* was present.

Megachilidae

Native megachilid species collected at BRF included the cleptoparasites *Stelis* (*Dolichostelis*) *louisae* (one female) and *Stelis* (*Stelis*) *nitida* (one female). The former is a colorfully marked parasite of native resin bees in subgenus *Megachile* (*Chelostomoides*), including *M.* (C.) *campanulae* (the likely host in NY and New England), which reaches its northern distributional limits in southern New York. *Stelis nitida* was described in 1878 from specimens collected in Canada and NY, but there have been few subsequent collections from eastern North America. It is most likely a northern and montane species that parasitizes *Osmia*, or possibly large *Hoplitis* species. Our sample of eight native *Osmia* species includes series of the forest-associated *O. bucephala* and *O. pumila*. We collected single specimens of three species that are scarce or absent in other recent collections from New York State, *O. collinsiae*, *O. felti*, and *O. inermis*. The last species, a probable oligolege of Ericaceae (M. S. Arduser, pers. comm.) previously unreported from NY, has also been identified among recent samples of bees from the Adirondacks (JSA and W. L. Romey, new record). Another *Osmia* species, *O. distincta*, has been found elsewhere in NY (e.g., South Hill Swamp, Ithaca, Tompkins County; and along the Hudson River) and in Pennsylvania to visit *Penstemon*, including *P. digitalis* Nutt. The tuft of curved hairs on the ocellar region of this species would seem to be an adaptation for collecting pollen from *Penstemon*, although *O. distincta* is apparently not a strict oligolege of this genus (M. Arduser, pers. comm.).

Our sample of native *Megachile* and associated *Coelioxys* cleptoparasites is impoverished, perhaps reflecting the inefficiency of bowl traps for capturing these strong-flying species (although Megachilini can be trapped in numbers in bowls of appropriate color, S. Droege, pers. comm.). The species captured are widely distributed and numerous across New York, excepting *M. montivaga*, which is known in the state from a few collections in southern NY (e.g., recently collected at Edmund Niles Huyck Preserve in Albany County). A report of this species from Ithaca (Leonard 1928) is based on a misidentified *M. inermis*.

Apidae, excluding bumble bees

Large and small carpenter bees were represented respectively by *Xylocopa virginica* (locally very numerous at BRF, but most uncollected) and by two abundant sister species of *Ceratina* (*Zadontomerus*), *C. calcarata* and *C. dupla*, that cannot be distinguished in the females. The related *C. strenua* Smith is also common in NY but was not collected.

All 18 identified species belonging to the *ruficornis* group of *Nomada* (=*Nomada s.str.*) in our samples are known or suspected to be cleptoparasites of *Andrena* species. Commonly encountered species of this group at BRF and other forested areas of the northeastern USA and southeastern Canada include the large, conspicuous species *N. luteoloides* (a valid species distinct from *N. sulphurata* Smith; see Schwarz and Gusenleitner 2004) and *N. maculata*, both cleptoparasites of large *Andrena* belonging to the subgenus *Melandrena* (Milickzy and Osgood 1995), and *N. bella*, a cleptoparasite of *A. imitatrix*. A new probable host association between *N. bella* and *A. imitatrix* was inferred by JSA (new information) based on repeated co-occurrence of these species at several sites across several years. Females of *N. bella* have been identified (M. Schwarz, pers. comm.) but remain undescribed. Further study of *Nomada* with bidentate mandibles (=*Gnathias* sensu Mitchell 1962) is needed to clarify separation of *N. bella* from *N. ovata*, *N. lepida*, and other similar species. We collected a single male *Nomada australis*, which is one of the three species belonging to the *erigeronis* group (=*Centrias*) known from NY. These are aestival cleptoparasites of *Agapostemon*.

Anthophora was represented by the wood-nesting species *A.* (*Clisodon*) *terminalis*, which is widely distributed and numerous in northern and montane forests from Siberia to eastern Canada [Davydova and Pesenko 2002; these authors distinguished the Holarctic *A. terminalis* from the Palearctic *A. furcata* (Panzer)].

Bumble bees

Black Rock Forest is a favorable habitat for bumble bees, and certain species were found in large numbers, especially *Bombus* (*Pyrobombus*) *impatiens* and its social parasite *B.* (*Psithyrus*) *citrinus* (also known to attack other *Bombus* species). Large numbers of *B. impatiens* in our late season samples reflect the unusually large colony size and long flight season (JSA has observed males flying as late as November 10 in Ithaca, NY, a colder locality than BRF) characteristic of this species. Other bumble bee species encountered include *B. perplexus* and *B. vagans*, both generally numerous in New York forests and bogs, and the widely distributed *B. bimaculatus* and *B. griseocollis*. We found few *B. vagans*, but the extremely similar (and thus infrequently identified) *B. sandersoni* was found in surprisingly large numbers, including series of queens, males, and workers. Two *Bombus ternarius* were found. This is a species of northern affinities found commonly south to the Catskills. Leonard (1928:1031–1032) regarded it as, "Essentially a Canadian and northern transition species...", and stated that "the species is not found near NYC. (Beq) [indicating J. Bequaert as the source]." Long-tongued bumble bee species belonging to subgenera *Fervidobombus* [*B. fervidus* (Fabricius) and *B. pensylvanicus* (Degeer)] and *Subterraneobombus* (*B. borealis* Kirby) that frequently visit clovers (especially *Trifolium*) were not collected. Absence of *B. fervidus* is surprising, but *B. pensylvanicus* has been scarce in NY in recent years and is no longer, "An abundant southern species, common as far north as central NY..." (Leonard 1928:1032). *Bombus borealis* has always been uncommon in New York State (Leonard 1928), and is generally absent from developed areas (e.g., it is unknown from the city of Ithaca, NY, but occurs in nearby countryside).

Absence of *Bombus* (*Bombus*) *affinis* in our sample of 1261+ bumble bee individuals is troubling because this species is well represented in historical collections from the northeastern United States, and is expected to be "...moderately abundant in the eastern to southern parts of the [New York] State..." (Leonard 1928: 1031). However, this species has recently disappeared from New York (e.g., from Ithaca and the NYC area, JSA, unpublished) and elsewhere (L. Day, pers. comm.). The regional

disappearance of *B. affinis* is coincident with an abrupt decline in *B.* (*Bombus*) *terricola* Kirby at Ithaca NY (Ascher, unpublished), and elsewhere (L. Day, pers. comm.), as well as the extirpation of the closely related *B.* (*Bombus*) *occidentalis* Greene from the San Francisco Bay Area and elsewhere in western North America, and the precipitous decline of the endangered *B.* (*Bombus*) *franklini* from its exceptionally restricted range in southern Oregon and northern California (Thorp 2005). Populations of *B. affinis*, and of all North American species of subgenus *Bombus*, and their obligate social parasites [e.g., *B.* (*Psithyrus*) *ashtoni*; a queen of this species was collected at BRF on June 13 1988, by J. G. Rozen], should be carefully monitored, as parasitism by *Nosema* and other parasites introduced and spread via the greenhouse trade in *Bombus* colonies poses a potentially severe threat to their survival.

Introduced bee species.—Our samples included numerous individuals of certain exotic bee species that have become established and locally invasive in eastern North America beginning in the 1990's.

Megachile sculpturalis, a giant resin bee native to northeastern Asia, was first collected in New York State in 1997 (Ascher 2001) and is now widely distributed and locally abundant in the Fingerlakes Region, and in southern NY, including NYC. Outside of New York, *M. sculpturalis* is now quite widely distributed and has recently been found in additional northeastern states such as Massachusetts (Martha's Vinyard, P. Gambino pers. comm.), Vermont, and New Hampshire (S. Droege, pers. comm.), as predicted by Hinojosa-Díaz et al. (2005).

The horn-faced mason bee *Osmia cornifrons*, native to eastern Asia including Japan, was deliberately introduced by USDA scientists as a managed pollinator of apples. After wide distribution and release, this species has recently established large populations in natural and urban (e.g., Manhattan and Brooklyn, NYC) habitats in the eastern United States to the point where it could be classified as invasive. We collected 66 specimens from on or around native vegetation and in bowls, and one female emerged from a trap nest. Non-specificity to orchards should not be surprising as *Osmia* (*Osmia*) species such as *O. cornifrons* and the closely related native species *O. lignaria* are polylectic, not specialists of fruit crops. In areas near where *O. cornifrons* were deliberately released (e.g., Patuxent National Wildlife Refuge, see Cane 2003), a very similar Asian species, *Osmia* (*Osmia*) *taurus* Smith has been found to be established. This species has also been found in Huntingdon County in south-central Pennsylvania (VG, new data), but not yet in NY.

We collected 10 *Anthidium oblongatum*, a species native to Europe and only recently detected in North America (Hoebeke and Wheeler 1999). This species is now abundant in the mid-Atlantic States, New York, and southern New England, usually in association with favored host plants such as *Lotus corniculata*, a weed generally distributed in waste places such as roadsides and abandoned lots, and *Sedum*.

The halictine species *Lasioglossum* (*L.*) *leucozonium* has long been present in North America and has therefore been generally regarded as native. However, its North American range is restricted to northeastern USA and southeastern Canada and does not include northwestern Canada or Alaska (see maps in McGinley 1986). This distributional pattern, and association of this species with introduced weeds such as *Chicorium* (Asteraceae), suggests that this ground-nesting species is adventive from Europe, not native as has been assumed. Molecular phylogenetic placement of *L. leucozonium* and *L. zonulum* (Smith) within the otherwise exclusively Old World *leucozonium* species group, and lack of significant genetic differences between Old and New World samples (see, e.g., Danforth and Ji 2001), further support the idea that the occurrence of these species in North

America is adventive. It is possible that these species were introduced in soil carried in ships' ballast as has been hypothesized for another ground-nesting bee species native to Europe and found in our study, *Andrena wilkella*. Extensive sampling of variable molecular markers such as COI is needed to test hypotheses of native vs. adventive origin for bee species with Holarctic distributions. *Megachile centuncularis* (L.) may be another early introduction from Europe, as this species has not been recorded in Alaska as would be expected for a species with a naturally Holarctic range.

Workers of *Apis mellifera* (L.) were abundant from mid-June and into October but were generally not collected.

Of the 144 bee species recorded in this study, six (4.2%) are exotic and 138 (95.8%) are native. Of the 6,543 specimens collected, 115 (1.7%) belong to exotic species, and 6,428 (98.2%) belong to native species.

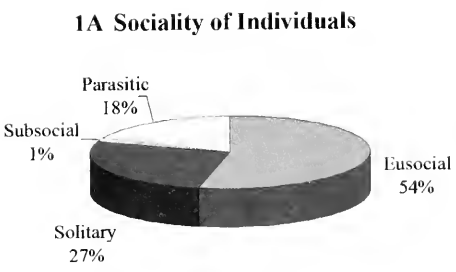
Wasps and other non-bees.—Our apoid wasp samples include 23 crabronid species (12 genera; Appendix 2). Some of these are generally numerous in forest edge habitats in New York such as *Ectemnius continuus*, which nests in holes in wood. Other species collected such as *Astata leuthostromi* and *Bicyrtes quadrifasciata* are ground-nesters that favor more open, often sandy habitats. Our vespid wasp sample includes long series of the native paper wasp *Polistes fuscatus*, both sexes of *Vespula consobrina*, a yellowjacket of northern (Canadian and Transition Zones) affinities, one individual of the rather scarce *Zethus spinipes*, and a variety of eumenines including cavity-nesting species found in our trap nests.

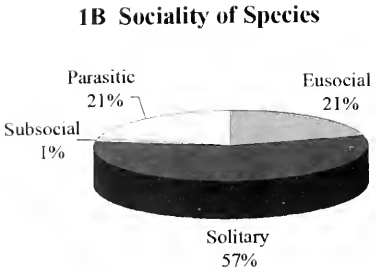
Ecological and behavioral patterns.—Ecological information (summarized in Appendix 1) was compiled for each of the 144 bee species from information found in catalogs and revisions, primary literature, and field observations, including those made during the BRF survey.

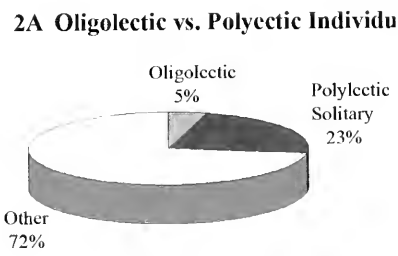
Of the 6,543 specimens collected, 5,364 (82.0%) belong to pollen collecting species, and 1,179 specimens (18.2%) belong to parasitic species (Fig. 1a). Of the 144 bee species recorded in this study, 116 (80.5%) are pollen-collecting species and 28 (19.4%) are parasitic (Fig. 1b). The abundance and diversity of parasites reflects a rich fauna of vernal *Nomada* associated with *Andrena* hosts. The preponderance of females (4321 vs. 1977 males vs. 245 of unrecorded sex) corresponds with the large number of workers of eusocial species, including the two most numerous species at BRF. Of the 6,543 bee specimens collected, 1,222 (18.7%) were *Augochlorella aurata* and 845 (12.9%) were *Bombus impatiens*. The sample of 1,113 bumble bees collected was dominated by *B. impatiens* (845, 75.9%) and its social parasite *B.* (*Psithyrus*) *citrinus* (154, 14.1%).

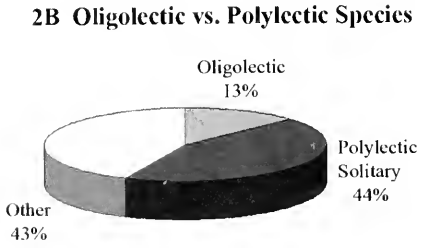
Seasonal patterns of occurrence can be obtained from Appendix 1, which gives extreme dates for BRF (by calendar date), NY as a whole (by month), and the entire North American range (by month) for each species. General patterns include an abundance and diversity of *Andrena* and their *Nomada* parasites at forest floor sites prior to leaf-out. At more open sites, seasonal turnover of the bee fauna was apparent, with notable peaks of abundance and species diversity corresponding with the bloom of favored plants such as *Vaccinium* in late spring (visited by, e.g., *Andrena* and *Osmia* spp.) and *Solidago* in late summer (visited by, e.g., *Colletes* spp., *Andrena simplex Pseudopanurgus andrenoides*, and the workers and males of the dominant eusocial species *Augochlorella aurata* and *Bombus impatiens*). Rather few oligolectic bee individuals were captured (292, 4.5% of the total) (Fig. 2a), but these represented a significant number of species in our sample (19, 13.2%) (Fig. 2b).

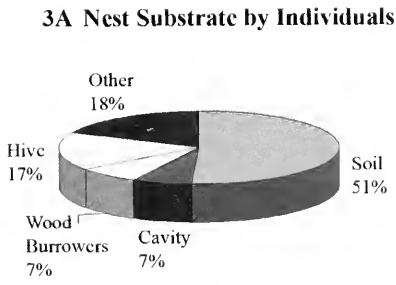
Although soil nesting individuals and species predominated in our samples, hive nesters, wood burrowers, and cavity-nesters were also well represented (Fig. 3a, b). Cavity-nesting species were numerous relative to the number of individuals, as

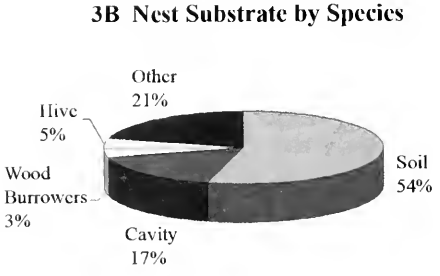


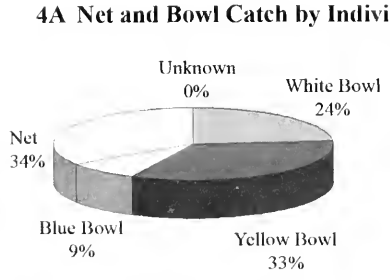


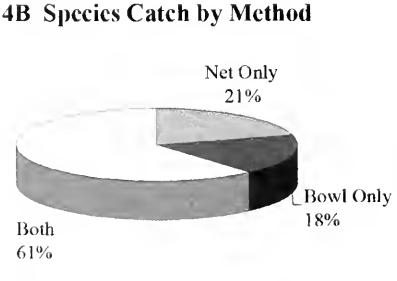












Figs 1–4. Summary of ecological properties of Black Rock Forest (BRF) bees. 1, Sociality. The category "solitary" includes communal species. Some individual nests or local populations of species categorized as "eusocial" may be solitary: 1A, percentage of individual bees belonging to each of the four recognized categories of sociality; 1B, percentage of bee species belonging to each of the categories. 2, Pollen specialization; those classified as oliglolectic are specialists that usually collect pollen from only a single family of plants; the polylectic category includes polylectic solitary bees only; those in the "other" category include parasites and social bees, which are necessarily generalists (i.e. polylectic): 2A, percentage of bee individuals that are

several cavity-nesters were represented by singletons or doubletons. By contrast, wood burrowing species were relatively few (Fig. 3b), although some of these species were captured in large numbers (e.g., *Augochlora pura*). The large number of hive-nesting individuals relative to species likely reflects their eusociality (see above).

A few species typical of more open and sandy areas were found at BRF (e.g., *Lasioglossum heterognathum, Bicyrtes, Astata*), but sand specialists such as *L. vierecki* were not found.

Efficacy and Biases of trapping methods.—The year 2003 was characterized by long periods of cold and cloudy weather and pans may have been particularly useful under these conditions as these allow catch during brief windows of sun on days when net-collecting would be unrewarding. Nearly twice as many individuals were bowl trapped than netted (4,322 vs. 2,221) (Fig. 4a), but the net sample was biased against certain of the most common and readily identified taxa (see above). Bowls were found to be particularly useful in forest and at the forest edge where flowers are few, dispersed, or in the case of trees and shrubs, difficult to reach. Where flowers are scarce, bowls may be particularly effective due to lack of competition from real flowers. Using bowls, we found certain inconspicuous forest-associated species rarely taken in nets such as *Stelis nitida*. Well known biases of bowl traps reinforced by our study include low catch rates for certain groups, especially fast and high-flying species of, e.g., *Colletes, Megachile*, and perhaps *Melissodes*, and high catch rates for slow and low-flying species of, e.g., small *Lasioglossum, Andrena, Osmia*, and *Nomada*. Our results generally support the currently accepted view that a combination of bowl trapping using multiple colors and netting is the best way to efficiently collect a plurality of species (S. Droege et al. protocol). Only 89 of the 144 bee species collected (61.8%) were collected by both nets and bowls, with 30 species (20.8%) unique to nets and 26 (17.6%) unique to bowls (Fig. 4b). The net collected sample was richer than the bowl trapped sample in total bee species (117 vs. 113) and in number of unique species (29, 20.4% vs. 25, 17.6%).

Although wood and cavity-nesting bees were numerous in this survey, only one individual bee (the introduced *Osmia cornifrons*) used our trap-nests. The poor performance of trap-nests might possibly be explained by an abundance of natural nesting substrates (standing dead wood) at BRF. Alternatively, bees may have been out-competed for the trap-nests by eumenines and *Trypoxylon*, or else the nests may have been placed in sites that ultimately proved to be too shady.

Comparison to other bee faunas.—In comparison to the bee fauna of NYS as a whole (423 species) and to the fauna of some well-sampled localities within the state such as Ithaca (274 species), the 144 species identified in our BRF sample is relatively few (Table 1). However, several of these records are of considerable biogeographic or ecological interest (see above). The NY bee fauna includes many species which are regionally rare and/or have highly specialized ecological requirements, and are therefore unlikely to be found at BRF.

←

oligolectic, polylectic and solitary, or other; 2B, percentage of bee species that are oligolectic, polylectic and solitary, or other. 3, Nest substrates: 3A, percentage of individuals belonging to each nesting category: soil, cavity, wood burrowers, hive, or other (primarily cleptoparasites that live in the nests of their hosts); 3B, percentage of bee species known or inferred to use the nest substrate indicated. 4, Collecting method: net vs. white bowl, vs. blue bowl, vs. yellow bowl: 4A, percentage of bee individuals caught by each method; 4B, percentage of bee species caught by net only vs. bowl only vs. both net and bowl.

Nonetheless, it seems highly probable that at least 250 bee species could be present at BRF based on totals of 274 species recorded from Ithaca, Tompkins County, NY (Ascher, unpublished), in a colder climate than BRF, and ca. 300 species recorded from the vicinity of Carlinville in southern Illinois (Robertson 1929, Marlin and LaBerge 2001), in seemingly unremarkable farm country.

The high number and proportion of singletons (28 spp., 19.4%), of doubletons (12 spp., 8.3%), of species known from a single sex (ca. 31 spp., ca. 21.0%) excluding *Lasioglossum*, and of rarely collected species (i.e., 3–10 individuals collected: 36 species, 25.3%), indicate that more prolonged and intensive surveying using the same methods would reveal many additional species, likely resulting in taxonomically and biogeographically significant specimens.

Another indication of the incompleteness of sampling of the total BRF fauna is that only 57.8% of the 249 bee species known from southern New York excluding NYC and Long Island (i.e., Sullivan, Ulster, and Dutchess, Orange, Putnam, Rockland, and Westchester, Counties) were found. These might be considered to represent a regional pool of species from an area relevant to BRF. The total of 249 species known from an area relevant to BRF is only 59% of the species total for New York State as a whole (423), which in turn is only 57% of the 743 bee species known from the eastern USA. Twenty additional species recorded in NY only from coastal NYC and Long Island (e.g., the coastal dune specialist *Lasioglossum marinum*) are less likely to occur at BRF.

Most bee species at BRF are widely distributed in NY and have been recorded from other well-collected sites such as Ithaca (123 species shared with BRF, 85.4% of the BRF total) and NYC (103 species shared with BRF, 71.5% of the BRF total). Northern elements of the fauna at BRF can be defined as those species known from the northern and montane portions of NY (e.g., the Adirondack Mountains and in most cases Ithaca), but absent from NYC, Long Island, and other warmer and coastal areas. Examples of northern species occurring at or near their southern limits at BRF and unknown from NYC include *Andrena rufosignata*, *A. algida*, *Stelis nitida*, *Osmia felti*, *O. inermis*, *Bombus ternarius*, and possibly *B. sandersoni* (southern distributional limits of this species remain uncertain due to identification difficulties versus *B. vagans*). Although these northern species are likely genuinely absent from NYC, many of the 42 species known from BRF, but not NYC may be found in the latter area when more thorough samples have been made of semi-natural habitats such as Pelham Bay Park. Southern elements in the BRF fauna include the following species that are unknown from the very well collected Fingerlakes Region (which includes Ithaca): *Lasioglossum bruneri*, *Andrena nuda*, *A. confederata*, *A. hilaris*, and *Melissodes subillata*. The apparent absence of these species from Ithaca and elsewhere in central and northern New York is probably genuine and likely reflects a real faunal difference from BRF. *Andrena violae* is another species of southern affinities that is very rare in Ithaca (see above).

The Sørensen index [$C_s = 2a/(2a + b + c)$ where a is the number of species shared between two sites, b is the number of species found at only one site, and c is the number of species found only at the other site] was used to quantify similarity between various sites. The total for BRF vs. Ithaca is 58.9% whereas the total for BRF vs. NYC is 58.2%. The similar Sørensen values for comparisons involving these two areas (despite BRF's much greater geographical proximity to NYC) reflect many shared widespread and northern species with Ithaca, and significant differences between BRF and NYC due to the presence of northern forest elements (e.g., blueberry associates) only at BRF and of coastal/sand associates only in NYC.

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Appendix 1. List of bee species collected at Black Rock Forest (BRF) in 2003. For family-group classification see Table 1. **BRF individuals**, the total number of individual bees recorded during the survey. Individual totals for certain *Nomada*, *Sphecodes*, and *Bombus* species may be imprecise as not all specimens could be determined with certainty. The notation [++] after *Xylocopa virginica* and *Apis mellifera* indicate that numerous additional individuals of these species were seen at BRF but not collected; the notation [+] indicates that we do not regard these *Nomada* species as singletons or doubletons as additional specimens of these species likely exist among the remaining undetermined specimens. **BRF flight period**, The first and last dates on which specimens were collected at BRF in 2003. **NY flight period**, The recorded flight period by month (numbered from 1–12) for NY as a whole based on study of all available collections. **Nearctic flight period**, The recorded flight period by month across the entire Nearctic range of the species. Certain anomalous records, such as late summer records for typical spring species, may be erroneous and have been ommitted from the totals. **NY abundance**, Perceived abundance in NY as a whole for each species found at BRF based on all available collections. In descending order: A=abundant, C=common, F=fairly common, U=uncommon, R=rare. Although subjective, these provide some context for the BRF records. Some species may prove to be more abundant than indicated when improved samples and identication tools become available. Some species indicated as uncommon or rare in New York, such as *Andrena violae*, are numerous in other states. **Native vs. exotic**, Each species is classified as native (N) or exotic (E) based on current and historical patterns of distribution. **Nest substrate**, The known or inferred nest substrate of each non-parasitic species is categorized as either soil (S), cavity (C; usually pre-existing, often in wood or pith, typically above-ground), wood burrowing (W; typically in rotting or soft wood); and hive (H). *Xylocopa virginica* (not placed in a category) burrows in hard wood. The nest sites of many species remain unknown but can be inferred based on nest substrates used by closely related species. **Sociality**, Each species is characterized as solitary (S), subsocial (B), eusocial (E), or parasitic (P). The behavior of many species remains unstudied but can be inferred based on the known behavior of closely related species. **Pollen specificity**, Each solitary, pollen-collecting species has been characterized as either oligolectic (pollen specialist; usually collecting pollen from flowers belonging to a single plant family) or polylectic (pollen generalist; regularly collecting pollen from more than one plant family). **New York**, An X indicates a verified record for New York City (i.e. the five boroughs). **Ithaca**, An X indicates a verified record within the city limits of Ithaca, Tompkins County.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Colletes compactus Cresson, 1868	3	Sep 30–Oct 16	8–10	7–11	C	N	S	S	O	X	X
Colletes simulans Cresson, 1868	1	Aug 28	7–10	1, 5–11	A	N	S	S	O	X	X
Hylaeus (Hylaeus) mesillae (Cockerell, 1896)	1	Aug 14	4–9	4–10	C	N	C	S	P	X	X
'Hylaeus (Prosopis) modestus Say, 1837	19	May 27–Sept 11	5–9	5–9	A	N	C	S	P	X	X
Hylaeus (Prosopis) modestus Say females [*or affinis* (Smith)]	125	June 24–Sept 29									
Augochloropsis (Paraugochloropsis) metallica (Fabricius, 1793)	23	June 10–Oct 1	5–10	3–11	C	N	S	S	P	X	X
Augochlorella aurata (Smith, 1853)	1222	April 24–Oct 1	4–10	4–10	A	N	S	E	–	X	X
Augochlora (Augochlora) pura (Say, 1837)	289	May 5–Oct 16	4–10	4–10	A	N	W	S	P	X	X
Agapostemon (Agapostemon) sericeus (Förster, 1771)	2	Aug 15–Sept 6	4–10	4–10	C	N	S	S	P	X	X
Agapostemon (Agapostemon) virescens (Fabricius, 1775)	7	May 9–Oct 1	5–10	5–10	C	N	S	S	P	X	X
Sphecodes johnsonii Lovell, 1909	2	Aug 14	8–10	8–10	U	N	–	P	–		X

Appendix 1. Continued.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Sphecodes fattigi Mitchell, 1956	3	Aug 15	8	8–10	R	N	–	P	–		
Sphecodes galerus Lovell & Cockerell, 1907	1	June 24	4–8	4–9	F	N	–	P	–	X	X
Sphecodes levis Lovell & Cockerell, 1907	1	May 18	5–8	5–8	U	N	–	P	–		X
Halictus (Odontalictus) ligatus Say, 1837	229	May 9–Oct 16	4–10	1–12	A	N	S	E	–	X	X
Halictus (Protohalictus) rubicundus (Christ, 1791)	4	May 18–July 26	3–9	3–9	C	N	S	E	–	X	X
Halictus (Seladonia) confusus Smith, 1853	39	May 18–Oct 1	4–10	4–10	A	N	S	E	–	X	X
Lasioglossum (Lasioglossum) acuminatum McGinley, 1986	2	May 9–June 10	5–7	4–10	F	N	S	S	P		
Lasioglossum (Lasioglossum) coriaceum (Smith, 1853)	1	Sept 6	4–9	3–10	A	N	S	S	P	X	X
Lasioglossum (Lasioglossum) fuscipenne (Smith, 1853)	1	July 8	5–10	3–12	F	N	S	S	P	X	
Lasioglossum (Lasioglossum) leucozonium (Schrank, 1781)	8	May 18–Sept 29	5–10	5–10	A	E	S	S	P	X	X
Lasioglossum (Evylaeus) cinctipes (Provancher, 1888)	4	June 24–July 26	4–9	3–9	C	N	S	E	–		X
Lasioglossum (Evylaeus) nelumbonis (Robertson, 1890)	21	July 8–Oct 1	6–9	3–11	F	N	S	S	O		
Lasioglossum (Evylaeus) quebecense (Crawford, 1907)	14	April 24–Aug 28	3–9	3–9	C	N	S	S	P	X	X
Lasioglossum (Dialictus) abanci (Crawford, 1932)	181	April 24–Sept 11	4–8	4–9	C	N	S	E	–		X
Lasioglossum (Dialictus) admirandum (Sandhouse, 1924)	24	May 9–Oct 1	4–9	3–9	A	N	S	E	–	X	X
Lasioglossum (Dialictus) albipenne (Robertson, 1890)	1	Sept 11	5–9	5–9	C	N	S	E	–		X
Lasioglossum (Dialictus) bruneri (Crawford, 1902)	24	May 9–Sept 11	4–10	2–10	C	N	S	E	–	X	
Lasioglossum (Dialictus) cattellae (Ellis, 1913)	9	May 9–Sept 11	5–9	5–9	F	N	S	E	–		
Lasioglossum (Dialictus) cephalotes (Dalla Torre, 1896)	1	May 5	5–9	5	U	N	–	P	–	X	
Lasioglossum (Dialictus) coeruleum (Robertson, 1893)	21	May 18–Sept 11	4–9	4–10	C	N	W	E	–	X	X
Lasioglossum (Dialictus) cressonii (Robertson, 1890)	58	April 24–Sept 11	4–9	3–10	C	N	W	E	–	X	X
Lasioglossum (Dialictus) divergens (Lovell, 1905)	1	July 8	6–7	6–7	C	N	S	S	P		X
Lasioglossum (Dialictus) foxii (Robertson, 1895)	59	April 16–July 8	4–7	4–9	C	N	S	S	P	X	X
Lasioglossum (Dialictus) heterognathum (Mitchell, 1960)	6	May 18–Sept 6	5–9	4–9	C	N	S	E	–		X
Lasioglossum (Dialictus) imitatum (Smith, 1853)	13	May 18–Oct 1	4–10	4–10	A	N	S	E	–	X	X
Lasioglossum (Dialictus) laevissimum (Smith, 1853)	20	May 9–Sept 21	3–9	3–10	C	N	S	E	–	X	X
Lasioglossum (Dialictus) lineatulum (Crawford, 1906)	53	April 24–Oct 1	4–10	4–10	A	N	S	E	–		X
Lasioglossum (Dialictus) lineatulum/rohweri	28	April 16–Aug 15									
Lasioglossum (Dialictus) michiganense (Mitchell, 1960)	1	Sept 29	6–9	6–9	R	N	–	P	–		

Appendix 1. Continued.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Lasioglossum (Dialictus) nigroviride (Graenicher, 1911)	3	Aug 28	4–8	4–10	C	N	S	E	–	X	X
Lasioglossum (Dialictus) nymphaearum (Robertson, 1895)	1	Aug 28	4–10	4–10	C	N	S	E	–	X	X
Lasioglossum (Dialictus) oblongum (Lovell, 1905)	102	May 9–Oct 1	4–9	3–10	C	N	W	E	–		X
Lasioglossum (Dialictus) pilosum (Smith, 1853)	1	July 8	4–10	2–10	A	N	S	E	–	X	X
Lasioglossum (Dialictus) rohweri (Ellis, 1915)	213	April 24–Sept 29	4–9	4–9	A	N	S	E	–	X	X
Lasioglossum (Dialictus) tegulare (Robertson, 1890)	169	May 9–Sept 29	4–10	1–12	C	N	S	E	–	X	X
Lasioglossum (Dialictus) versans (Lovell, 1905)	4	June 2–Sept 11	4–9	4–10	C	N	S	E	–		X
Lasioglossum (Dialictus) undet.	188	April 24–Oct 1									
Andrena (Andrena) carolina Viereck, 1909	113	May 5–June 24	5–6	4–7	C	N	S	S	O	X	X
Andrena (Andrena) cornelli Viereck, 1907	1	May 27–Sept 11	5–6	4–7	U	N	S	S	O	X	X
Andrena (Andrena) frigida Smith, 1853	3	April 24	3–5	2–7	C	N	S	S	O	X	X
Andrena (Andrena) mandibularis Robertson, 1892	3	May 9–May 27	4–6	3–7	C	N	S	S	P	X	X
Andrena (Andrena) milwaukeensis Graenicher, 1903	15	April 14–June 10	4–7	3–8	C	N	S	S	P	X	X
Andrena (Andrena) rufosignata Cockerell, 1902	14	April 14–June 2	4–6	4–8	C	N	S	S	P		X
Andrena (Andrena) tridens Robertson, 1902	2	May 5–May 27	3–5	3–7	F	N	S	S	P		
Andrena (Callandrena s.l.) krigiana Robertson, 1901	7	June 2–June 10	5–7	3–7	F	N	S	S	O		
Andrena (Callandrena s.l.) simplex Smith, 1853	10	Sept 11–Oct 16	8–9	7–9	C	N	S	S	O		X
Andrena (Cnemidandrena) hirticincta Provancher, 1888	3	Aug 28–Sept 21	8–9	8–10	C	N	S	S	O	X	X
Andrena (Cnemidandrena) nubecula Smith, 1853	5	Aug 14–Sept 29	7–10	7–10	C	N	S	S	O	X	X
Andrena (Conandrena) bradleyi Viereck, 1907	82	April 16–May 27	4–6	3–9	F	N	S	S	O	X	
Andrena (Derandrena) ziziaeformis Cockerell, 1908	2	May 18–June 2	4–6	4–6	U	N	S	S	P		
Andrena (Euandrena) algida Smith, 1853	1	April 16	3–6	3–8	F	N	S	S	P		X
Andrena (Gonandrena) fragilis Smith, 1853	8	June 10–June 24	5–7	5–7	C	N	S	S	O	X	X
Andrena (Holandrena) cressonii Robertson, 1891	20	April 14–June 24	4–6	3–8	A	N	S	S	P	X	X
Andrena (Iomelissa) violae Robertson, 1891	3	May 9–June 2	5–6	4–7	R	N	S	S	O		X
Andrena (Larandrena) miserabilis Cresson, 1872	38	April 16–June 24	3–7	1–7	A	N	S	S	P	X	X
Andrena (Melandrena) carlini Cockerell, 1901	157	April 14–June 10	3–6	3–7	C	N	S	S	P	X	X
Andrena (Melandrena) confederata Viereck, 1917	1	June 10	6	2–6	U	N	S	S	P	X	
Andrena (Melandrena) dunningi Cockerell, 1898	2	May 9–May 18	3–6	2–7	A	N	S	S	P	X	X

Appendix 1. Continued.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Andrena (Melandrena) hilaris Smith, 1853	2	May 27–June 10	5	3–7	U	N	S	S	P	X	
Andrena (Melandrena) nivalis Smith, 1853	4	May 27–June 10	4–7	2–8	F	N	S	S	P		X
Andrena (Melandrena) pruni Robertson, 1891	36	May 5–July 8	5–6	3–6	F	N	S	S	P	X	X
Andrena (Melandrena) vicina Smith, 1853	22	May 9–June 24	4–6	3–7	A	N	S	S	P	X	X
Andrena (Plastandrena) crataegi Robertson, 1893	44	May 18–June 24	5–7	3–8	A	N	S	S	P	X	X
Andrena (Rhacandrena) robertsonii Dalla Torre, 1896	53	May 9–July 26	5–7	4–8	C	N	S	S	P	X	X
Andrena (Scaphandrena) arabis Robertson, 1897	5	May 5–June 10	4–6	4–5	C	N	S	S	O	X?	X
Andrena (Scrapteropsis) alleghaniensis Viereck, 1907	4	June 2–June 10	5–7	4–7	C	N	S	S	P	X	X
Andrena (Scrapteropsis) imitatrix Cresson, 1872	58	April 14–June 24	3–6	3–7	A	N	S	S	P	X	X
Andrena (Simandrena) nasonii Robertson, 1895	67	May 5–June 10	4–6	3–7	A	N	S	S	P	X	X
Andrena (Taeniandrena) wilkella (Kirby, 1802)	20	May 27–Aug 14	4–8	4–9	A	E	S	S	P	X	X
Andrena (Thysandrena) bisalicis Viereck, 1908	8	April 14–June 10	3–6	2–9	F	N	S	S	P	X	X
Andrena (Trachandrena) ceanothi Viereck, 1917	3	May 18–June 24	5–6	5–6	F	N	S	S	P	X	X
Andrena (Trachandrena) forbesii Robertson, 1891	4	April 24–June 24	4–6	4–6	C	N	S	S	P	X	X
Andrena (Trachandrena) hippotes Robertson, 1895	1	May 18	4–6	4–6	C	N	S	S	P	X	X
Andrena (Trachandrena) nuda Robertson, 1891	38	May 18–June 24	4–6	4–6	F	N	S	S	P	X	
Andrena (Trachandrena) rugosa Robertson, 1891	52	April 16–June 24	4–6	4–6	A	N	S	S	P	X	X
Andrena (Trachandrena) spiraeana Robertson, 1895	3	July 8–July 26	6–8	6–8	F	N	S	S	P	X	X
Andrena (Tylandrena) perplexa Smith, 1853	4	May 18–June 10	4–6	3–6	C	N	S	S	P	X	X
Calliopsis (Calliopsis) andreniformis Smith, 1853	4	July 8–Aug 15	6–8	4–10	C	N	S	S	P	X	X
Pseudopanurgus andrenoides (Smith, 1853)	21	Aug 28–Oct 16	8–10	8–10	C	N	S	S	O	X	X
Anthidium (Proanthidium) oblongatum (Illiger, 1806)	10	July 17–Sept 11	6–10	6–10	A	E	S	S	P	X	X
Stelis (Dolichostelis) louisae Cockerell, 1911	1	July 26	7–8	3–10	U	N	–	P	–		
Stelis (Stelis) nitida Cresson, 1878	1	June 24	6–7	6–7	R	N	–	P	–		X
Heriades (Neotrypetes) carinatus Cresson, 1864	25	July 8–Aug 28	6–9	4–9	C	N	C	S	P	X	X
Hoplitis (Alcidamea) producta (Cresson, 1864)	5	June 10–July 26	5–7	4–7	C	N	C	S	P		X
Hoplitis (Monumetha) spoliata (Provancher, 1888)	2	July 8–July 26	6–8	4–8	F	N	C	S	P		X
Osmia (Melanosmia) atriventris Cresson, 1864	16	May 9–Aug 14	4–7	4–7	C	N	C	S	P		X
Osmia (Melanosmia) bucephala Cresson, 1864	30	May 9–July 8	4–6	4–6	C	N	C	S	P	X	X

Appendix 1. Continued.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Osmia (Melanosmia) collinsiae Robertson, 1905	1	May 18	4–6	4–6	U	N	C	S	P		X
Osmia (Melanosmia) distincta Cresson, 1864	1	June 24	5–6	5–6	F	N	C	S	P		X
Osmia (Melanosmia) felti Cockerell, 1911	1	May 9	5–6	6	R	N	C	S	P		X
Osmia (Melanosmia) inermis (Zetterstedt, 1838)	1	June 24	5–7	5–7	U	N	C	S	O		
Osmia (Melanosmia) inspergens Lovell & Cockerell, 1907	9	June 2–July 26	5–6	5–6	F	N	C	S	P		X
Osmia (Melanosmia) pumila Cresson, 1864	145	April 24–July 8	4–7	4–7	C	N	C	S	P	X	X
Osmia (Osmia) cornifrons (Radoszkowski, 1887)	65	April 24–June 24	4–6	4–6	C	E	C	S	P	X	X
Osmia (Osmia) lignaria Say, 1837	4	April 24–May 18	3–6	3–6	C	N	C	S	P	X	X
Megachile (Callomegachile) sculpturalis Smith, 1853	3	Sept 6	6–9	6–9	C	E	C	S	P	X	X
Megachile (Chelostomoides) campanulae (Robertson, 1903)	5	July 26–Sept 6	6–9	2–11	C	N	C	S	P	X	X
Megachile (Litomegachile) mendica Cresson, 1878	15	July 8–Sept 11	5–10	5–10	C	N	C	S	P	X	X
Megachile (Megachile) montivaga Cresson, 1878	1	Sept 11	7–9	4–9	U	N	C	S	P	X	
Megachile (Megachile) relativa Cresson, 1878	11	June 24–Sept 11	5–9	5–10	C	N	C	S	P	X	X
Megachile (Sayapis) pugnata Say, 1837	1	July 26	6–9	6–9	F	N	C	S	O	X	X
Megachile (Xanthosarus) gemula Cresson, 1878	11	June 2–July 26	6–8	4–8	F	N	C	S	P		X
Coelioxys (Boreocoelioxys) octodentata Say, 1824	1	Aug 24	6–9	5–10	C	N	–	P	–	X	X
Coelioxys (Cyrtocoelioxys) modesta Smith, 1854	1	July 17	6–8	6–8	F	N	–	P	–	X	X
Xylocopa (Xylocopoides) virginica (Linnaeus, 1771)	2[++]	June 10–Aug 14	3–10	3–10	C	N	–	B	–	X	X
Ceratina (Zadontomerus) calcarata Robertson, 1900	63	May 9–Sept 11	3–10	3–10	A	N	C	B	–	X	X
Ceratina (Zadontomerus) dupla Say, 1837	21	May 18–Sept 11	4–9	4–9	C	N	C	B	–	X	X
Ceratina (Zadontomerus) calcarata/dupla	61	May 18–Sept 21									
Nomada australis Mitchell, 1962	1	June 10	5–6	4–6	U	N	–	P	–	X	
Nomada bella Cresson, 1863	67	April 14–May 18	3–4	3–4	C	N	–	P	–		X
Nomada cressonii Robertson, 1893	38	May 9–June 24	4–7	4–7	C	N	–	P	–	X	X
Nomada cuneata (Robertson, 1903)	13	May 27–June 24	5–6	5–6	F	N	–	P	–		X
Nomada denticulata Robertson, 1902	35	May 9–July 26	5–6	5–6	F	N	–	P	–	X	X
Nomada depressa Cresson, 1863	2[+]	May 18–June 10	4–7	4–7	F	N	–	P	–		X
Nomada illinoensis Robertson, 1900	3	May 5–May 18	4–6	4–6	F	N	–	P	–	X	X
Nomada lehighensis Cockerell, 1903	7	April 16–June 2	4–6	4–6	F	N	–	P	–		X

Appendix 1. Continued.

Species	BRF individuals	BRF flight period	NY flight period	Nearctic flight period	NY abundance	Native vs. Exotic	Nest Substrate	Sociality	Pollen specificity	New York City	Ithaca
Nomada lepida Cresson, 1863	2[+]	May 9–June 24	5–7	5–7	C	N	–	P	–	X	X
Nomada luteoloides Robertson, 1895	38	May 5–June 24	4–7	4–7	C	N	–	P	–	X	X
Nomada maculata Cresson, 1863	61	April 24–June 24	4–6	4–6	C	N	–	P	–	X	X
Nomada ovata (Robertson, 1903)	104	May 9–June 24	5–6	5–6	F	N	–	P	–	X	X
Nomada parva Robertson, 1900	1	May 18	4–6	4–6	U	N	–	P	–		X
Nomada perplexa Cresson, 1863	34	April 16–June 24	6–7	6–7	F	N	–	P	–	X	X
Nomada pygmaea Cresson, 1863	35	May 5–July 26	4–6	4–6	C	N	–	P	–	X	X
Nomada sayi Robertson, 1893	1[+]	May 18	4–7	4–7	F	N	–	P	–	X	X
Nomada xanthura Cockerell, 1908	12	April 24–June 10	4–6	4–6	F	N	–	P	–		X
Nomada ruficornis group undet. without tooth	118	April 14–June 24									
Nomada ruficornis group with tooth (*Gnathias sensu* Mitchell)	29	May 9–June 24									
Melissodes (Eumelissodes) denticulata Smith, 1854	2	Aug 28	7–9	5–10	F	N	S	S	O	X	X
Melissodes (Eumelissodes) subillata LaBerge, 1961	2	July 26	7–8	6–9	F	N	S	S	O	X	
Anthophora (Clisodon) terminalis Cresson, 1869	8	July 8–Sept 6	6–9	5–9	C	N	W	S	P	X	X
Bombus (Psithyrus) citrinus (Smith, 1854)	157	May 18–Oct 1	5–10	5–10	C	N	–	P	–	X	X
Bombus (Separatobombus) griseocollis (DeGeer, 1773)	1	July 8	4–9	2–10	C	N	H	E	–	X	X
Bombus (Pyrobombus) bimaculatus Cresson, 1863	76	May 5–July 26	4–9	2–9	C	N	H	E	–	X	X
Bombus (Pyrobombus) impatiens Cresson, 1863	845	April 16–Oct 16	4–11	1–11	A	N	H	E	–	X	X
Bombus (Pyrobombus) perplexus Cresson, 1863	61	April 24–Aug 14	4–10	4–10	C	N	H	E	–	X	X
Bombus (Pyrobombus) sandersoni Franklin, 1913	110	April 14–Oct 16	4–10	4–10	U	N	H	E	–		
Bombus (Pyrobombus) ternarius Say, 1837	2	June 10–Sept 21	4–10	4–10	C	N	H	E	–		X
Bombus (Pyrobombus) vagans Smith, 1854	4	Sept 29–Oct 16	5–10	5–10	C	N	H	E	–	X	X
Bombus (Pyrobombus) undet.	5	June 24–Sept 29									
Apis (Apis) mellifera Linnaeus, 1758	9[++]	June 2–Oct 16	2–12	1–12	A	E	H	E	–	X	X

Appendix 2. List of wasp species collected incidentally at BRF in 2003.

Family	Subfamily	*Species*
Crabronidae	Astatinae	*Astata leuthstromi* Ashmead, 1897
Crabronidae	Bembecinae	*Bicyrtes quadrifasciata* (Say, 1824)
Crabronidae	Bembecinae	*Gorytes deceptor* Krombein, 1958
Crabronidae	Crabroninae	*Ectemnius (Clytochrysus) lapidarius* (Panzer, 1804)
Crabronidae	Crabroninae	*Ectemnius (Ectemnius) atriceps* (Cresson, 1865)
Crabronidae	Crabroninae	*Ectemnius (Ectemnius) borealis* (Zetterstedt, 1838)
Crabronidae	Crabroninae	*Ectemnius (Ectemnius) dives* (Lepeletier & Brullé, 1834)
Crabronidae	Crabroninae	*Ectemnius (Hypocrabro) continuus* (Fabricius, 1804)
Crabronidae	Crabroninae	*Ectemnius (Hypocrabro) decemmaculatus* (Say, 1823)
Crabronidae	Crabroninae	*Ectemnius (Hypocrabro) stirpicola* (Packard, 1866)
Crabronidae	Crabroninae	*Liris (Leptolarra) argentata* (Beauvois, 1811)
Crabronidae	Crabroninae	*Lyroda subita* (Say, 1837)
Crabronidae	Crabroninae	*Trypoxylon (Trypargilum) lactitarse* Saussure, 1867
Crabronidae	Crabroninae	*Trypoxylon (Trypoxylon) frigidum* Smith, 1856
Crabronidae	Crabroninae	*Trypoxylon (Trypoxylon) pennsylvanicum* Saussure, 1867
Crabronidae	Pemphredoninae	*Pemphredon (Cemonus) inornata* Say, 1824
Crabronidae	Pemphredoninae	*Pemphredon (Cemonus) rugifera* Dahlbom
Crabronidae	Pemphredoninae	*Mimumesa nigra* (Packard, 1867)
Crabronidae	Pemphredoninae	*Psen erythropoda* Rohwer, 1910
Crabronidae	Pemphredoninae	*Pseneo simplicicornis* (Fox, 1898)
Crabronidae	Philanthinae	*Cerceris atramontensis* Banks, 1913
Crabronidae	Philanthinae	*Cerceris fumipennis* Say, 1837
Crabronidae	Philanthinae	*Cerceris halone* Banks, 1912
Crabronidae	Philanthinae	*Philanthus gibbosus* (Fabricius, 1775)
Sphecidae	Sphecinae	*Isodontia (Isodontia) philadelphica* (Lepeletier, 1845)
Sphecidae	Sphecinae	*Isodontia (Murrayella) mexicana* (Saussure, 1867)
Vespidae	Eumeninae	*Parancistrocerus pedestris* (Saussure, 1855)
Vespidae	Eumeninae	*Parancistrocerus pensylvanicus* (Saussure, 1855)
Vespidae	Eumeninae	*Parancistrocerus perennis* (Saussure, 1857)
Vespidae	Eumeninae	*Euodynerus foraminatus* (Saussure, 1853)
Vespidae	Eumeninae	*Euodynerus hidalgo* (Saussure, 1857)
Vespidae	Eumeninae	*Euodynerus leucomelas* (Saussure, 1855)
Vespidae	Eumeninae	*Ancistrocerus adiabatus* (Saussure, 1852)
Vespidae	Eumeninae	*Ancistrocerus antilope* (Panzer, 1798)
Vespidae	Eumeninae	*Ancistrocerus campestris* (Saussure, 1852)
Vespidae	Eumeninae	*Ancistrocerus waldenii* (Viereck, 1906)
Vespidae	Eumeninae	*Symmorphus (Symmorphus) canadensis* (Saussure, 1855)
Vespidae	Eumeninae	*Eumenes (Eumenes) fraternus* Say, 1824
Vespidae	Eumeninae	*Zethus (Zethus) spinipes* Say, 1837
Vespidae	Polistinae	*Polistes dominulus* (Christ, 1791)
Vespidae	Polistinae	*Polistes fuscatus* (Fabricius, 1793)
Vespidae	Vespinae	*Dolichovespula arenaria* (Fabricius, 1775)
Vespidae	Vespinae	*Dolichovespula maculata* (Linnaeus, 1758)
Vespidae	Vespinae	*Vespula consobrina* (Saussure, 1864)
Vespidae	Vespinae	*Vespula flavopilosa* Jacobson, 1978
Vespidae	Vespinae	*Vespula germanica* (Fabricius, 1793)
Vespidae	Vespinae	*Vespula maculifrons* (Buysson, 1905)
Vespidae	Vespinae	*Vespula vidua* (Saussure, 1854)
Scoliidae	Scoliinae	*Scolia (Discolia) bicincta* Fabricius, 1775
Pompilidae	Ceropalinae	*Ceropales maculata* (Fabricius, 1775)

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The Biology and Morphology of *Entedon sylvestris* (Hymenoptera: Eulophidae), a Larval Endoparasitoid of *Ceutorhynchus sisymbrii* (Coleoptera: Curculionidae)

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Abstract.—The biology and morphology of preimaginal stages of *Entedon sylvestris* Szelényi (Hymenoptera: Eulophidae), are described in detail for the first time. *Entedon sylvestris* is a larval endoparasitoid of the seed-feeding larvae of the weevil *Ceutorhynchus sisymbrii* Dieckmann on the small tumbleweed mustard, *Sisymbrium loeselii* L. (Brassicaceae). In the Ukraine, females of *E. sylvestris* begin ovipositing in late May and continue to lay eggs until the beginning of July. Females of *E. sylvestris* parasitize weevil larvae of various instars. The parasitoid larva remains within the body of the host weevil larva until the emergence of the latter from the dried host-plant pods. The morphology of each of the three larval instars is described in detail. The moult of the parasitoid larva into the final instar, as well as pupation, takes place underground. Adults of *E. sylvestris* must therefore penetrate a soil layer to emerge the following spring.

Key words.—Entedoninae, larval endoparasitoids, parasitoid-host relationships, preimaginal morphology, *Sisymbrium loeselii*

Parasitic wasps of the genus *Entedon* Dalman (Eulophidae, Entedoninae) are endoparasitoids of immature stages of beetles. Curculionidae (including Scolytinae), Brentidae (including Apioninae), Anobiidae, Chrysomelidae (including Bruchinae), Buprestidae, Cerambycidae, Mordellidae, and Nitidulidae are recorded as hosts (Bouček and Askew 1968, Graham 1971, Askew and Kopelke 1989, Rasplus 1991). *Entedon ergias* Walker has been imported from Europe into North America for the biological control of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham) (Peck 1963). For some species, parasitism rates and/or general descriptions of the larval morphology are given (Ferrière 1939, Erdös 1944, Abedin and Quayum 1972, Tiwari 1976). However, these descriptions lack many morphological details, especially for the first instar larvae. Beaver (1966) and Fisher (1970) gave the most complete bioassays and reported egg-larval parasitism for *Entedon ergias* Walker, *E. rumicis* Graham, *E. pharnus* Walker. Askew (1991) and Gumovsky (1997) provided some information on percentage parasitism, the biology of the final instar larva and pupation procedure of *E. cioni* Thomson, *E. cionobius* Thomson and *E. zanara* Walker.

In general, despite some thorough reviews (Parker 1924, Parker and Thomson 1925) and occasional detailed descriptions (e.g., Darling 1992, 1995) of the larvae of Chalcidoidea, our knowledge of morphology of preimaginal stages of chalcid wasps is incomplete. Most discussions on larval morphology and biology concern ectoparasitoids, whereas endoparasitoid larvae traditionally attract less attention, mainly due to the difficulties with their preparation and identification. The larvae of Eulophidae were classified by Parker (1924) in group II (the ectoparasitoid forms) and V (egg endoparasitoids), differing mostly in having spiracles (group II) or being apneustic (group V). Later, when

discussing the morphological peculiarities of the first instar larvae of *Anastatus* sp. (Eupelmidae) and *Miscogaster* sp. (Pteromalidae), Parker and Thomson (1925) stated that some endoparasitoid larvae represent a transitional type between the groups corresponding to groups V and VI sensu Parker (1924).

The larval morphology of *Entedon* species is even more vague. The papers of Beaver (1966) and Fisher (1970) are the only sources of comprehensive descriptions of preimaginal stages, but these concern mainly the size, body proportions and number of spiracles, and are illustrated mostly by diagrammatic figures. Many of the minute morphological structures (e.g. sensorial organs) remain obscure and undescribed.

Weevils of the subfamily Ceutorhynchinae have a wide range of host plants, but many are restricted to Brassicaceae. Some Ceutorhynchinae species have gained special attention as pests of economically important plants (e.g., *Ceutorhynchus napi* Gyllenhal, *C. pallidactylus* (Marsham) and *C. obstrictus* (Marsham) damaging cabbage and oilseed rape in North America). Other species (e.g. *C. merkli* Korotyaev, *C. cardariae* Korotyaev, *C. alliariae* Brisout, *C. roberti* Gyllenhal) are under investigation as potential biological control agents against some introduced weeds (i.e. whitetops *Cardaria* spp., garlic mustard *Alliaria petiolaria*: Hinz *et al.* 2004, Hinz and Gerber, 1998). The small tumbleweed mustard, *Sisymbrium loeselii* L., is a plant of European origin that was accidentally introduced into the New World, and is now recorded in 31 states of the USA, and is regarded as an invasive weed (Stubbendieck et al. 1994).

Some parasitoid species (e.g. *Tersilochus* spp., *Microctonus* spp.) have been released in North America to control *Ceutorhynchus* spp. (e.g. *C. obstrictus*) that are pests of economic plants (e.g. *Brassica* spp.). However, parasitoids—unless sufficiently host-specific—could hamper the effectiveness of the *Ceutorhynchus* spp. released as biological control agents. It is therefore of vital importance to determine the parasitoid-host associations of Ceutorhynchinae and host plant preferences in various geographic regions.

This paper reports results obtained from and the methodological approaches used during the study of the parasitoid-host relationships between *Entedon sylvestris* Szelényi and its host, the weevil *Ceutorhynchus sysimbrii* Dieckmann on *Sisymbrium loeselii*, which is the first host record for the parasitoid.

MATERIALS AND METHODS

Adults of *Entedon sylvestris* were collected in the field on plants of *Sisymbrium loeselii* during late June and early July in 1995, 1997, 2001, 2002, 2004 in Kiev (50°28′N; 30°32′E) and Kherson oblast of Ukraine (v. Lazurnoe) (46°04′N; 32°29′E). Collections were made by both sweeping and capture of individual adults in tubes. Females were kept in Petri dishes and fed with diluted honey.

Mature pods of *S. loeselii* infested by the larvae of *Ceutorhynchus sysimbrii* (living inside the pods and feeding on seeds) were exposed to females of *E. sylvestris* kept in various reservoirs (Petri dishes, sealed plastic bags or boxes). Infestation by the weevil was indicated by the presence of a distinct hole in the pod made by the female's rostrum before oviposition.

The sites where the parasitoid's oviposition took place were marked with black ink. To study the morphology of the different larval instars of *E. sylvestris*, weevil larvae were removed from the pods at regular intervals and dissected. Endoparasitoid larvae found were fixed in Bouin's fixing solution (15 cm^3 picric acid (saturated), 5 cm^3 formaldehyde solution, 1 cm^3 acetic acid) to keep their original shape, and further washed out in 96–98% ethanol.

Mature weevil larvae, leaving the pods of their host plant, were put into plastic tubes (50 × 16 mm) filled 3/4–4/5 with

soil taken from field sites of *S. loeselii*. The behavior of the mature weevil larvae was observed through the transparent walls of the tubes. In September/October, when the pupae of *E. sylvestris* were expected to be completely formed, all tubes were carefully searched for earthen cells or dead weevil larvae. Dead weevil larvae found, were put into 5–10% solution of lactic acid to regain their original shape and soften. The softened larvae were then dissected in order to find the parasitoid larvae, in particular, the final instar larvae. These were transferred into lactic acid solution of higher concentration (40–70%) to obtain maximum swelling. The parasitoid larvae were then put into Bouin's fixing solution in order to fix the regained shape and then washed out in 96–98% ethanol.

All fixed larvae were kept in 100% ethanol for one day and then in 100% molecular sieved ethanol for maximal dehydration. After absolute ethanol the specimens were Critical Point Dried. The minute parasitoid larvae were put into pipette tips of various diameters sealed on the sides with cotton wool plugs, to avoid their loss during drying. The dried parasitoid larvae were transferred to SEM stubs on metallic pins, using static electrical charges to avoid damaging their extremely soft integuments. Finally the specimens were coated with gold and observed using a Scanning Electronic Microscope LEO 1530VP in the Max-Planck Institute for Metal Research, Stuttgart (MPI).

Field and laboratory video recordings were made using either 8 mm VP-A800 Pal Samsung Video Camera or with digital imaging of Leica IC A Videomodule integrated in the Leica MZ 125 stereomicroscope, using the video grabbing option conducted in Adobe Photoshop 6.0 programme through the use of the Falcon\Eagle Frame Grabber. The alignment of the photos corresponding to different layers in focus was conducted using the Combine Z programme Version 3.9 (designed by Alan Hadley, http://www.hadleyweb.pwp.blueyonder.co.uk/CombineZ/CombineZ3.zip).

RESULTS

Taxonomy

Entedon sylvestris Szelényi, 1981

Entedon sylvestris Szelényi, 1981: 277; *Entedon sylvestris* Szelényi; Askew, 1992: 119; *Entedon* (*Entedon*) *sylvestris* Szelényi; Gumovsky, 1999: 142; *Entedon sylvestris*; Gumovsky, Boyadzhiev, 2003: 23.

Material examined.—Types: Holotype female, paratypes 10 females, 6 males, Hungary, Hortobagy National Park (Szelényi) (Hungarian Museum of Natural History, Budapest); more than 2,000 specimens from Kiev (June 1995, 1997, 2003, 2002, 2004) and v. Lazurnoe (Kherson oblast), Ukraine, collected on plant shoots and fruits of *S. loeselii*; 7 females, 4 males, Kiev vicinity, Velyka Oleksandrivka, swept from *Berteroa incana* and *Capsella bursa-pastoris*, 31.V.2004, (Schmalhausen Institute of Zoology, Kiev); 54 females, 1 male, Kyiv, Trukhaniv Island, "Park Druzhby Narodiv", 24.VI.1995, swept from *Sisymbrium loeselii* (Natural History Museum, London); 1 female, 1 male, Gießen, ex *Capsella* seeds V.1995 (Weiffenbach) (Zoologische Staatssammlung Munchen).

Recent literature.—*Entedon sylvestris* has gained little attention since its description (Szelényi, 1981). This species belongs to the assemblage of the *cyanellus* and *costalis* species groups in having the anterior margin of the clypeus produced (Figs 1A, C, E, cly; 2C).

Askew (1992) reported it for Great Britain, presented a short corrected diagnosis and reported the possession of traces of pale strips on the fore tibiae. He also proposed to locate this species in the *cyanellus* species group of *Entedon* based on the presence of these hardly discernible foretibial strips and the 3-segmented funicle of the male. Gumovsky (1999), when revising the *cyanellus* group of the genus, argued against Askew's placement of *E. sylvestris* based on that only about 20% of specimens in a population possess

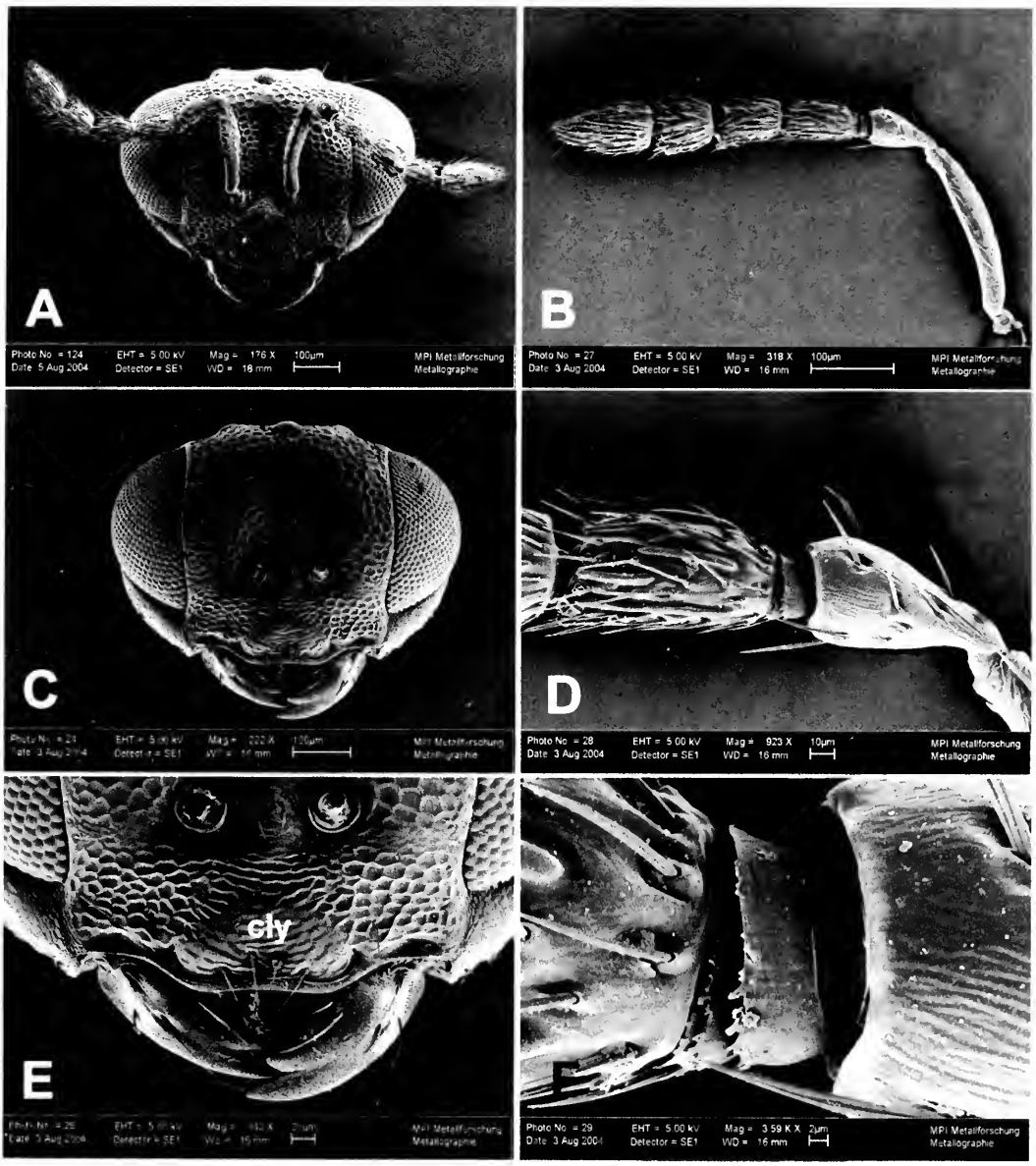

Fig. 1. *Entedon sylvestris*, female, details of morphology: A, C, head in frontal view; B, antenna; D, pedicel and 1st funicular segment; E, lower face; F, anelli; cly, clypeus.

the dim foretibial stripes, whereas the majority of the specimens have fore tibiae largely darkened, and proposed instead to accommodate *E. sylvestris* in the *costalis* species group (decreasing the value of the 3-segmented funicle of male as a species-group character). Gumovsky and Boyadzhiev (2003) reported this species for Bulgaria and also provided its comparative diagnoses in their key to species.

Comparative notes.—Within the European fauna, *E. sylvestris* can easily be confused with *E. cyanellus* and *E. fufius*. From the former species, *E. sylvestris* is easily distinguishable as female has a shorter 1st

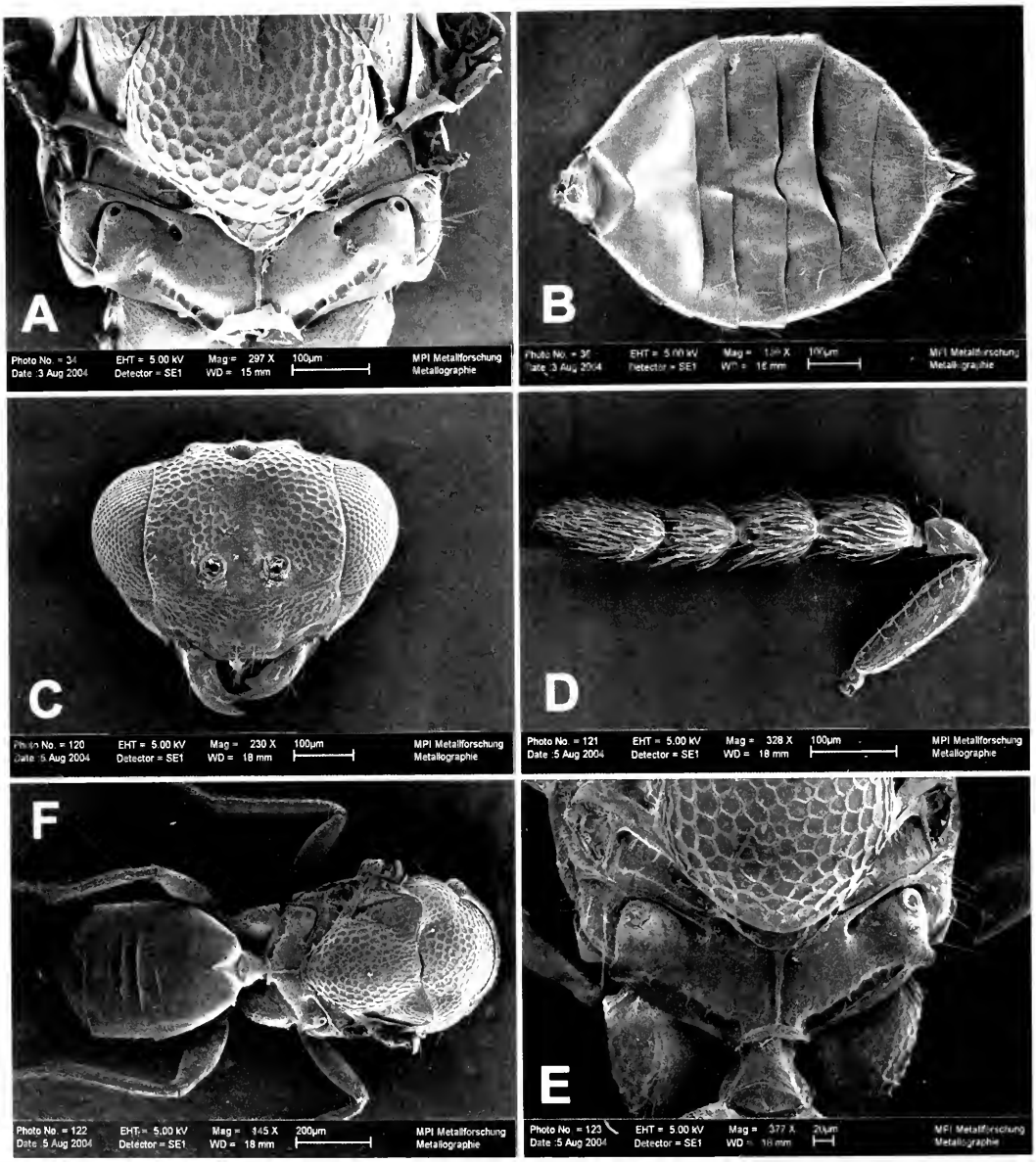

Fig. 2. *Entedon sylvestris*: A, B, female: A, posterior mesosoma; B, metasoma; C–F, male: C, head in frontal view; D, antenna; E, posterior mesosoma and anterior metasoma (petiole); F, body.

funicular segment (1.5–1.6 times as long as broad, Figs 1B, D, whereas in *E. cyanellus*—1.8–5.0 times) and by the narrower antennal scape of males (3.8 times as long as broad, Fig. 2D, about 3.0 times in *E. cyanellus*). Also, the foretibial stripes (when present) are much narrower and not terminated by a pale area on the distal end of the tibia (the tibia is always with distal pale band in *E. cyanellus*). The distal pale bands on the tibiae also distinguish *E. sylvestris* from *E. fufius* in which all tibiae are completely dark. Also, the 1st funicular segment of females is about 2.2 times as long as broad and 1.4 times as long as the 2nd segment in *E. fufius*, whereas in *E.*

sylvestris the segment is 1.5–1.6 times as long as broad and just slightly (about 1.1 times) longer than the 2nd (Figs 1B, D). Moreover, all flagellar segments are free in males of *E. fufius* (the funicle is 4-segmented), whereas in *E. sylvestris* the funicle is 3-segmented and two last funicular segments are closely attached (forming the 2-segmented clava, Fig. 2D).

Distribution.—Hungary (Szelényi 1981), Britain (Askew 1992), Bulgaria (Gumovsky and Boyadzhiev 2003), Ukraine (Gumovsky 1999).

Ecology

The host, Ceutorhynchus sisymbrii *Dieckmann.—Ceutorhynchus sisymbrii* is similar to *C. pulvinatus* Gyllenhal, 1837 in having dense coverage of dorsum and black rostrum, but differs from that species in that only the tibiae are red, not the entire legs (L. Behne, pers. comm.). Despite *C. sisymbrii* (Dieckmann 1966) being described nearly fifty years ago, its biology remained unknown. Dieckmann (1972) mentioned that studies on the life cycle of this species are of special value. Below I propose a brief synopsis of the field and laboratory observations on this species.

Adults of *Ceutorhynchus sisymbrii* (Figs 3A, B) feed on shoots, flowers and fresh seeds of *Sisymbrium loeselii*. Oviposition takes place in May–July. The female of the weevil lays its eggs into the pods of the host plant when the seeds are fully grown, but still soft and green (mature seeds are yellow to orange and hard). At first, the female makes an opening in the pod with her rostrum. It deeply penetrates the rostrum into the pod (up to the base of the rostrum) and eats the seed below the hole. Then the female turns back and presses its caudal end into the prepared opening, and begins oviposition. This behaviour is discernable by the rhythmic pulsing of her gaster. Occasionally, the female fails to aim into the prepared hole and lays an egg directly onto the surface of the plant pod. She then eats the egg, as in other weevil species (Kozlowski 2003).

The larvae feed on the seeds and remain in pods until they are fully grown (Figs 3C, D, E; Figs 11A, B). The pods then split and the mature larvae fall to the ground (Fig. 11D). Larvae leave the host plant's pods at the end of June – beginning of July. They quickly bury themselves into the soil, where they prepare an earthen cell, in which they pupate (Fig. 11E). I have found adult beetles in the dissected earthen cells in October. However, I assume that adult weevils are already present before, but leave their soil/earthen cocoons only the following spring.

Host searching and oviposition of the parasitoid, E. sylvestris.—The females of *E. sylvestris* can be found in the field from late May until early July (Figs 4A–G). The parasitoid female searches along the pods of *S. loeselii* for weevil larvae, by drumming the pod surface with her antennae (Fig. 4A). Once she has located a host, she walks back and forth several times before starting to oviposit. She bends her gaster downwards and briefly hooks the ovipositor saw into the plant tissues. She then releases the gaster so that it strengthens in a position perpendicular to the ovipositor (Figs 4B, C). Thereafter she penetrates the pod wall with her ovipositor, and carries out rhythmic, twisting movements to find the weevil larva, as in other parasitoid species. Oviposition lasts about 30–90 seconds. Quite often the ovipositor penetration causes the host's haemolymph to exude, and then females of *E. sylvestris* feed on these excretions.

Immature stages of *E. sylvestris*

Egg.—Elongate, white to transparent, without discernible sculpture. No stalks or terminal bulbous projections, reported by Beaver (1966) for *E. ergias*, were found. Size, about 260–300 μm long and about 80–100 μm wide.

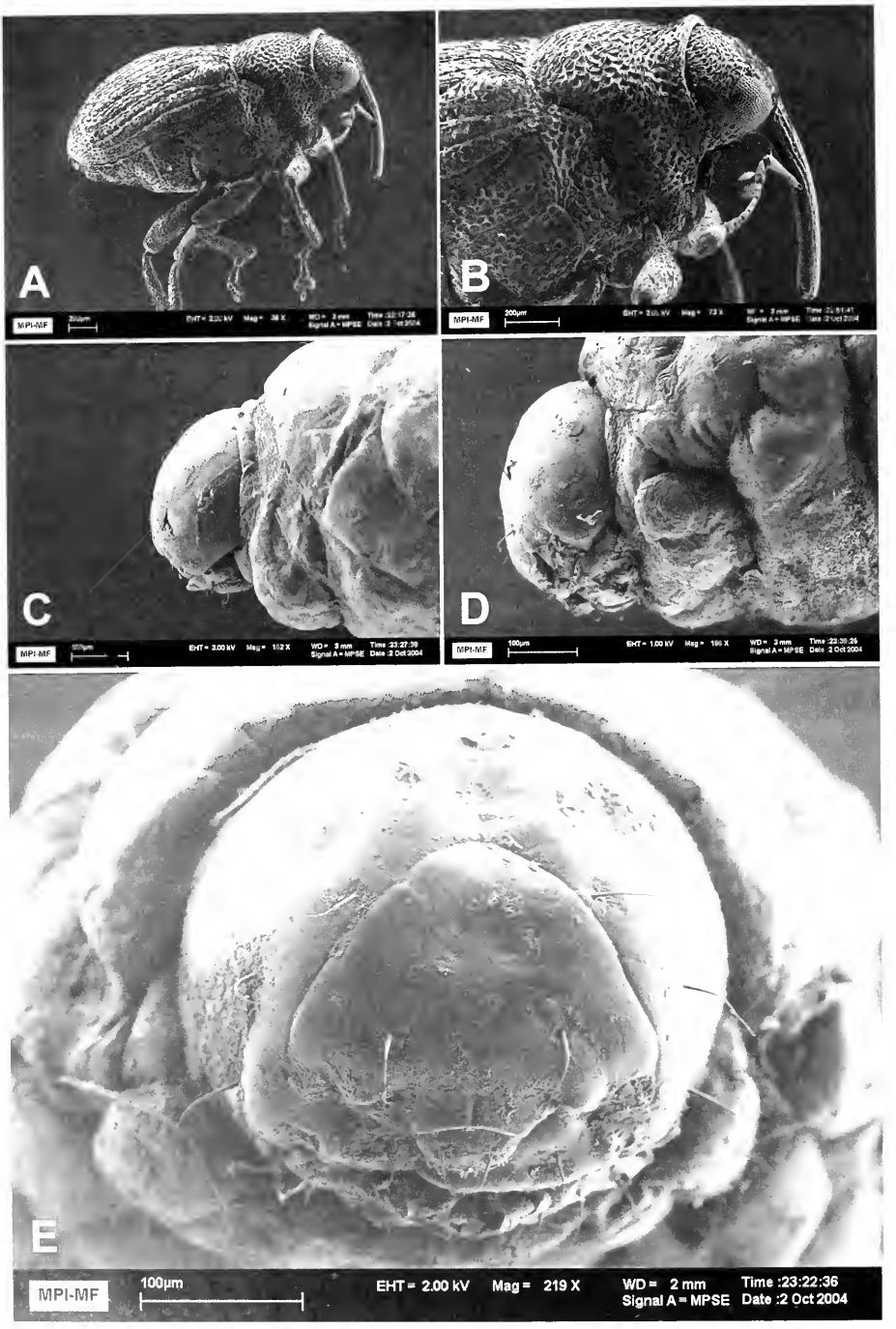

Fig. A–E. *Cleutorhynchus sisymbrii*. A, B, female, C–E, mature larva.

1st instar larva.– Habitus. The first instar larva of *E. sylvestris* is hymenopteriform, pale (nearly transparent), has 13 body segments and a cranium. There are some different forms, which were found during dissection of the host larvae. One is "slim" (Figs 5A, 6A), about 300 µm long and about 104 µm wide (max.), and another

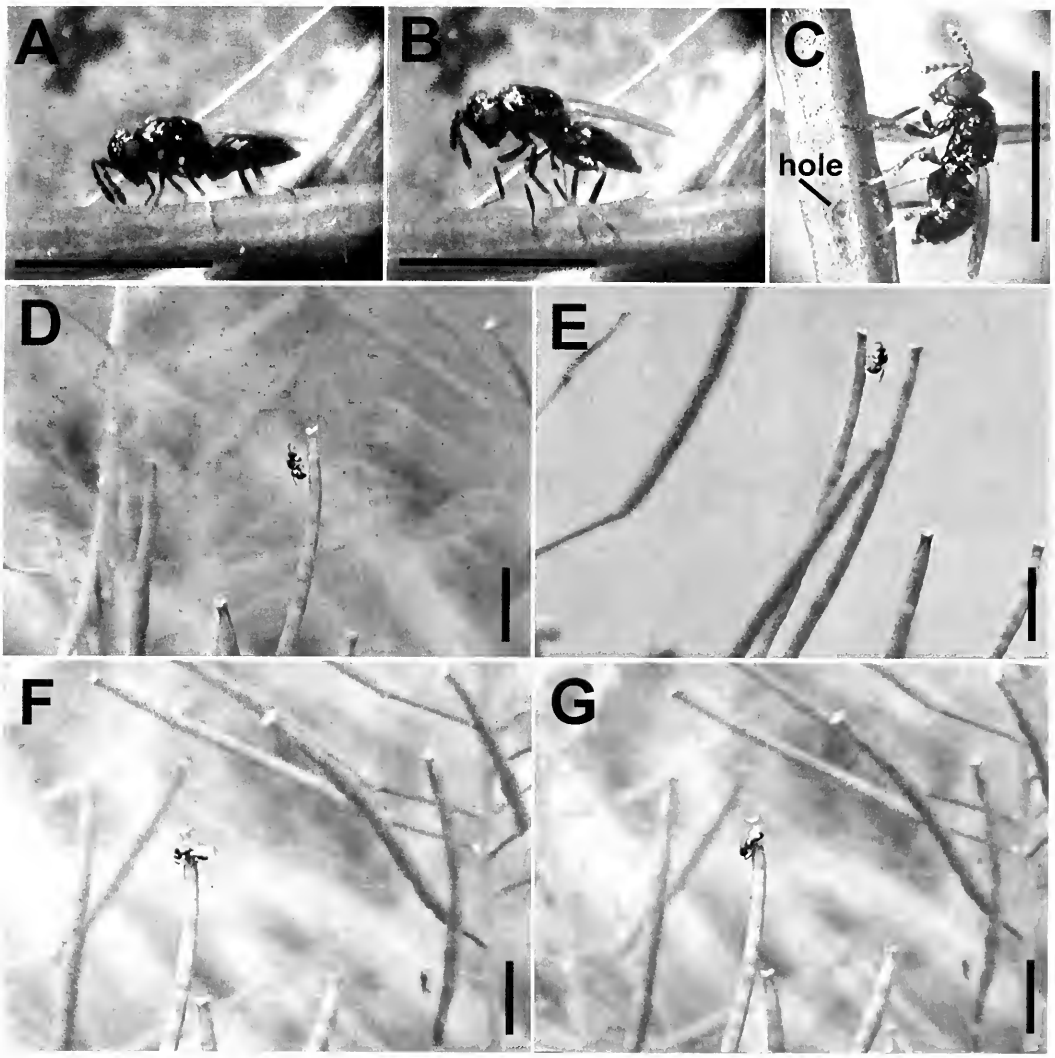

Fig. 4. A–G, the female of *Entedon sylvestris* oviposits into the larva of *Ceutorhynchus sisymbrii* in pods of *Sisymbrium loeselii*: A–C, in laboratory; D–G, in the field; hole, oviposition hole of weevil female. Scale bars: A–C, 2 mm; D–G, 5 mm.

form is "swollen" (Figs 6E, F), about 450 µm long and about 206 µm wide. Occasionally, specimens of an intermediate form were found (Fig. 6G), with a length of about 260 µm and a maximum width of about 108 µm. Despite the differences in size, I regard all three forms as belonging to the same larval instar, because of the possession of the peculiar shape of the head capsule (cranium) and body surface. The different body proportions are probably caused by different nutritional conditions, and fixation and drying circumstances.

Body segments. The last, XIIIth, segment bears sharp triangular tubercles along its margin, arranged in two or three rows in the shape of a crown (Figs 6C, D). These tubercles are very distinct in freshly emerged larvae, but occasionally are coated with secretions (Fig. 6H). These rows of tubercles are also distinct in the "swollen" larvae (Fig. 6H), however, they are not so clearly distinguishable in these larvae due

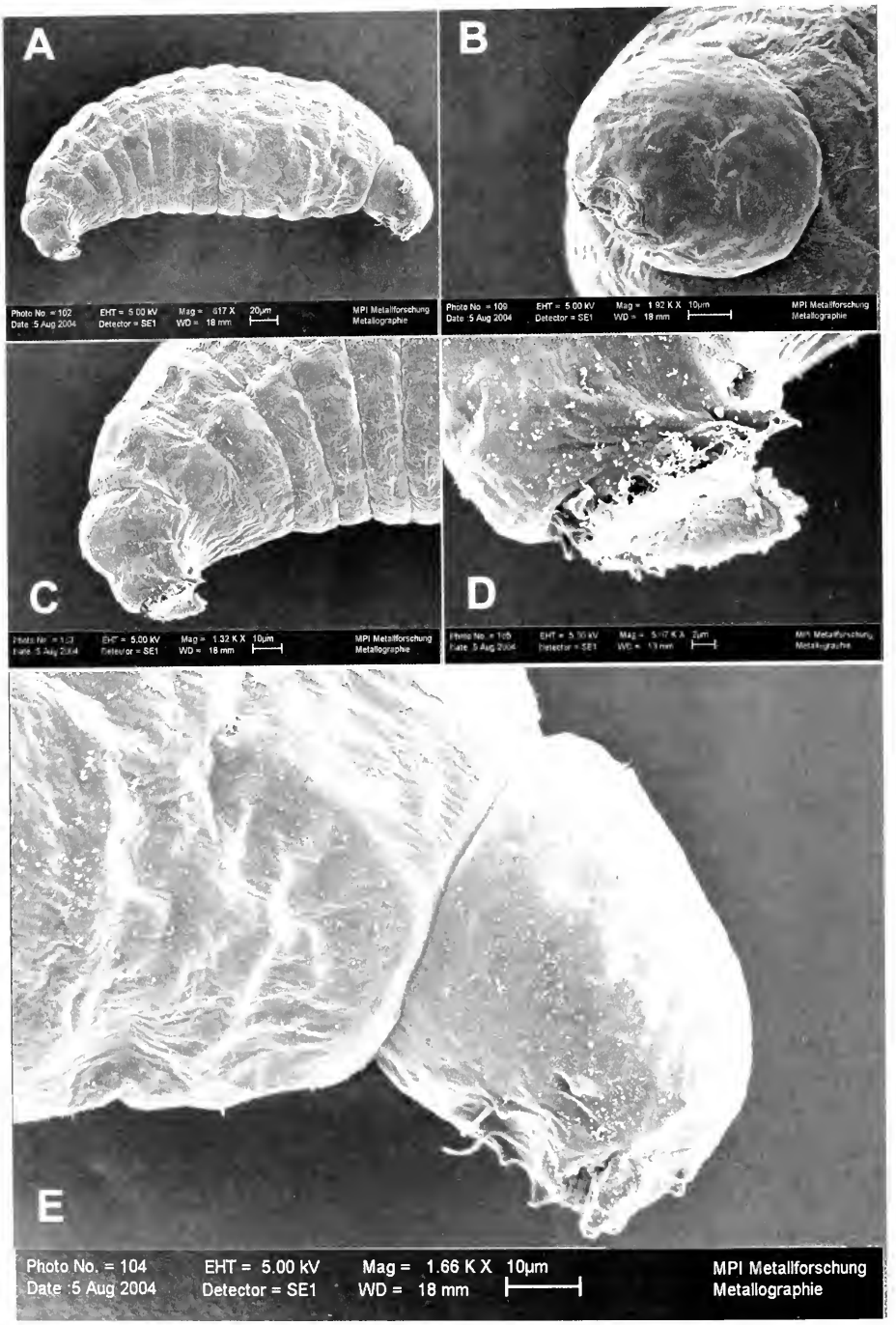

Fig. 5. *Isodontia*, first-instar larva: A, habitus; B, E, head close-up; C, D, cauda close-up.

to the thickness of the preceding segment (Figs 6E, F, H). Segments IV–XII bear distinct dorsal semicircular serrations (Fig. 6C, se) along their anterior margins, which consist of small curved teeth. Segments I–III bear no distinguishable teeth or serration, which reflects the subdivision into thoracic (I–III) and abdominal (IV–

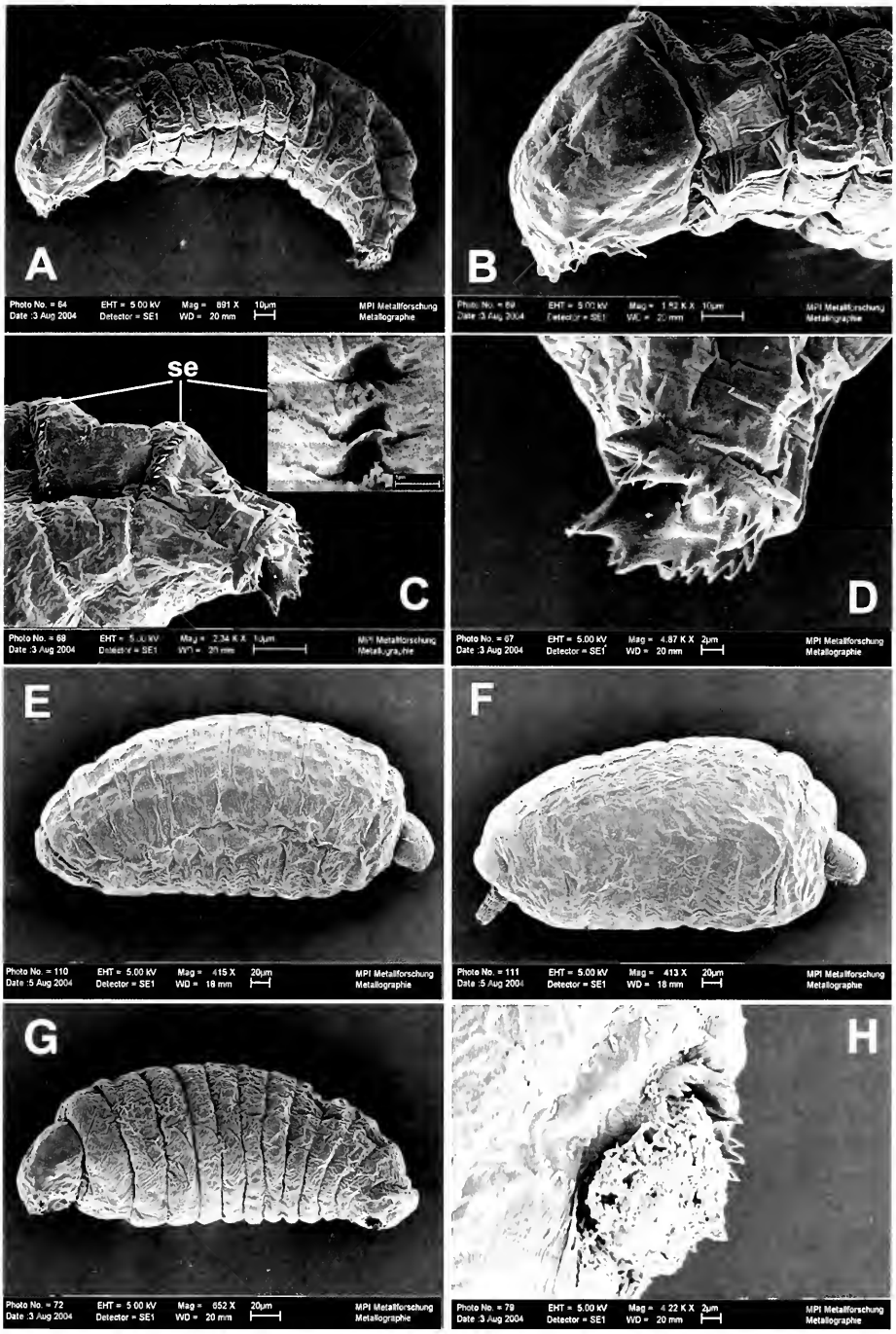

Fig. 6. *E. sylvestris*, first-instar larva: A, E–G, habitus; B, head; C, D, H, cauda; se, serration.

XIII) segments. No spiracles were found on the body of the larvae.

Head capsule (cranium). The head capsule is weakly sclerotized, narrowing ventrally, with a characteristic "beak"-shaped end, which is formed by the protruding palpi of the labrum. In light microscopy, the labrum adopts an active backward and

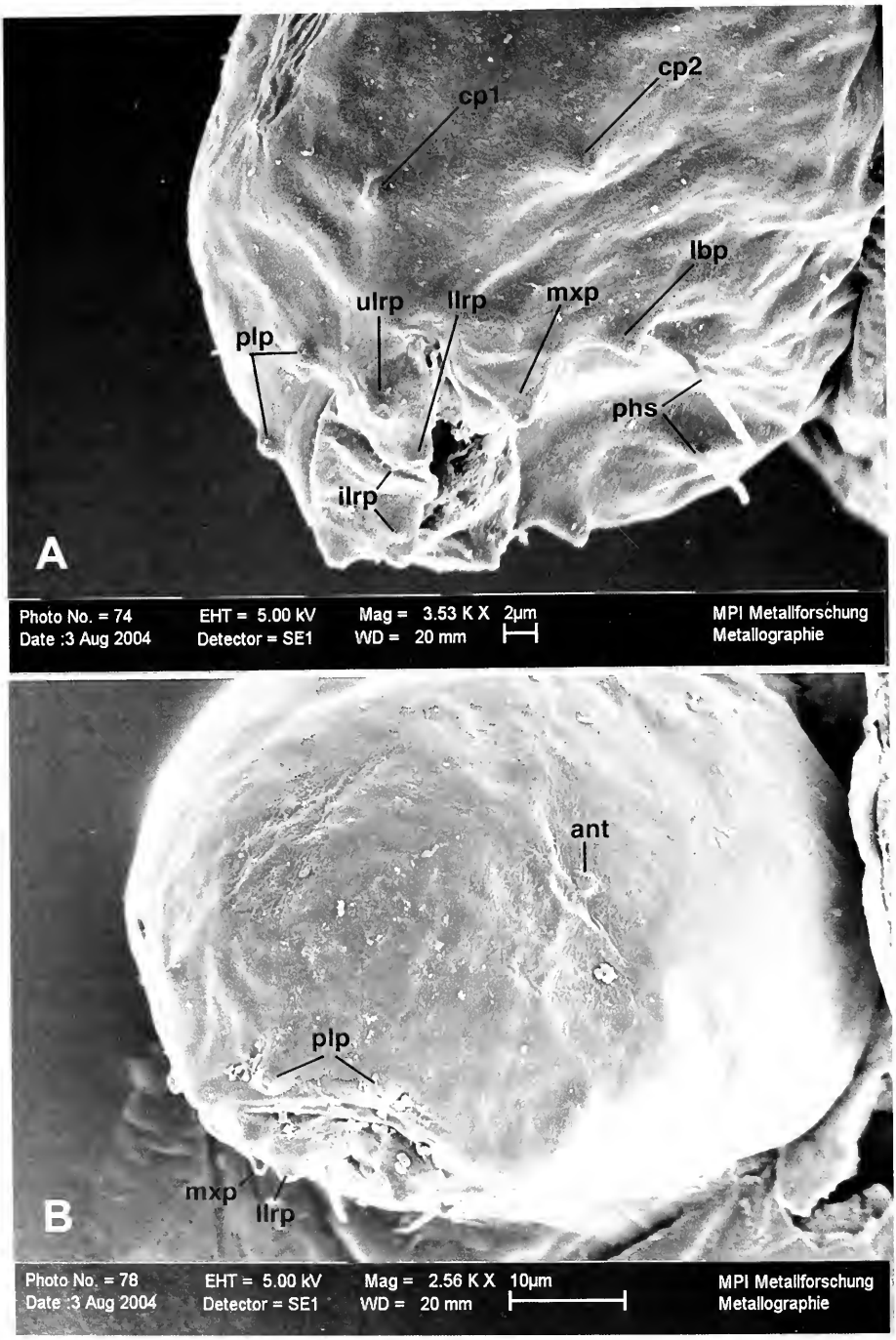

Fig. 7. *Leptofoenus*, first-instar larva, details of the head morphology (see text for abbreviations).

forward motion. Antennae are absent, indicated only as small swellings on the upper part of the head capsule. The sensorial structures of the head are well-developed and arranged in a relatively fixed position (Figs 7, 8). The lateral area of the cranium bears three pairs of cranial palpi: the upper (cp1), the lower (cp2) and

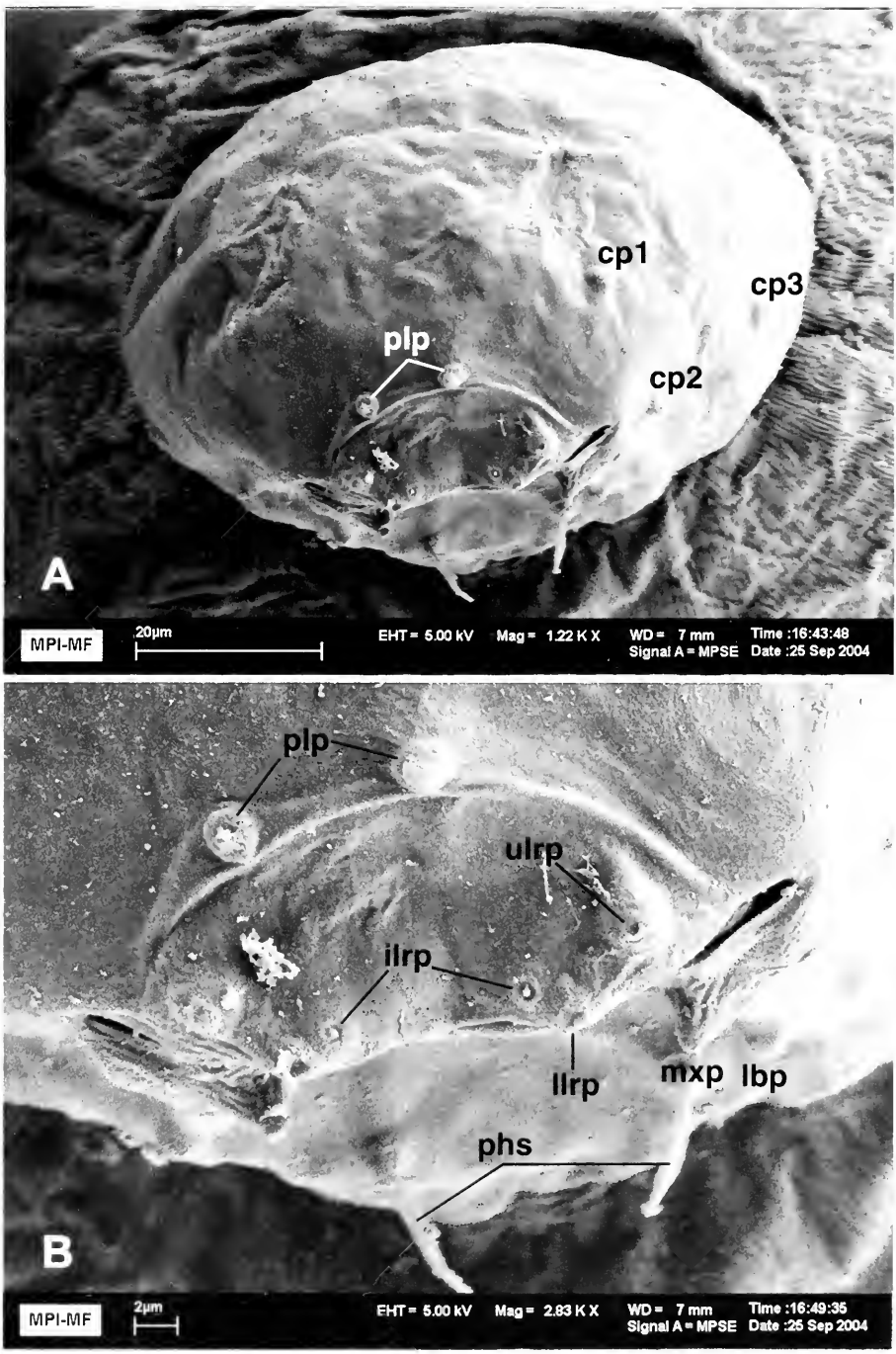

Fig. 8. *E. sylvestris*, first-instar larva, details of the head morphology (see text for abbreviations).

the posterior (cp3) palpi. There is a pair of enlarged pleurostomal palpi (plp) just above the labrum. The labrum bears 3 pairs of labral palpi (grouped by one from each side): the upper lateral labral palpi (ulrp), the lower lateral labral palpi (llrp) and the inner labral palpi (ilrp). A large palpus is located near each maxilla (mxp)

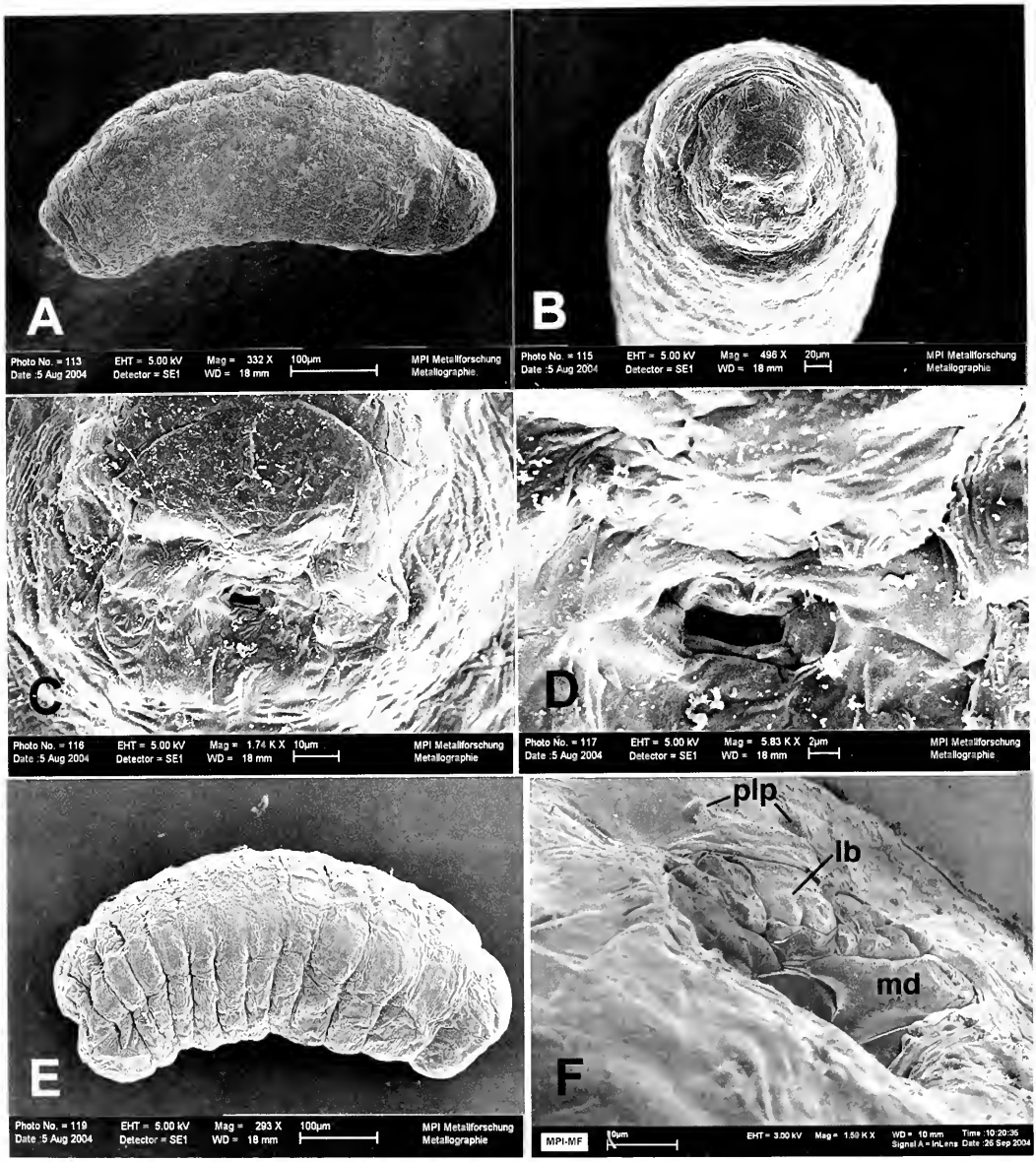

Fig. 9. *E. sylvestris*, second-instar larva, details of morphology: A, E, habitus; B, head in frontal view; C, head close-up; D, mouth area, close-up; F, mouth area, lateral view; plp, pleurostomal palpi; lb, labrum, md, mandible.

and behind them there is a pair of smaller labial palpi (lbp). A pair of comparatively long pharyngeal setae (phs) is situated behind the latter palpi.

2nd instar larva.—The second instar larva of *E. sylvestris* is also hymenopteriform and pale, with similar body segmentation (13 body segments and the head capsule), 500–590 µm long. However, the proportions and shape of the segments are different: the larva is more robust (Figs 9A, E) and none of the segments has serrations. The last segment bears no "caudal crown". The head is more spherical and the sensorial structures of the head are less clear (Figs 9C, D). However, it is still possible

to discern the pleurostomal palpi, the delimited labrum and short mandibles (about 20 µm long). No spiracles are recognizable.

Final instar larva.—Dissections of the dead host larvae revealed two forms of the parasitoid larvae, which differ from each other by their size and body shape. The smaller form fits the size range and morphological peculiarities of the second instar larva, described above. The larger form found within the body of the dead, buried host larvae, were 0.96–1.02 mm long (Fig. 10A), which is nearly twice as long as the second instar, but still nearly half of the average length of the pupa (1.8 mm). It has large (46 µm long) and heavily sclerotized (dark brown in color) mandibles and discernible hypostome (Figs 10D, F). I regard these peculiarities to be specific to the final instar. The sensory structures of the head are hardly distinguishable, apart from large antennae situated on broad swellings (Figs 10B, C). Spiracles were difficult to distinguish because the skin of the larva was too shriveled. The large antennae are peculiar to the final instar larvae of Chalcidoidea (Parker 1924). Fisher (1970) also draws the large round areas (equivalent to the large antennae) on the upper part of the head of the final instar larva of *E. rumicis*, but does not mention them in the text. The possession of large antennae is one of the characters supporting the assumption that this is the final instar larva of *E. sylvestris*. The smaller body size of the larva is probably artificial and resulted from incomplete swelling of the dried, dead larvae.

Pupa.—Generally, pupation takes place in the host's earthen cell (Fig. 11F). Sometimes, pupae could be found directly in soil samples, which suggest that parasitoid pupation can also take place without the successful creation of an earthen cell by the host. In the laboratory, the host's earthen cells and the "free" pupae were found 2–3 centimeters from the upper soil level (the overall height of the soil level in tubes was about 3 cm), and the host larvae can probably pupate even deeper.

The pupa is black, obtect, with distinct outlines of head, mesosoma, metasoma, wings, legs and antennae. The average length is 1.8–1.9 mm, the width of the head is about 0.6–0.7 mm, of mesosoma – 0.8 mm, of metasoma – 0.9 mm. The last larval skin, covered by soil particles, is often attached to the caudal end of the pupa.

Parasitoid-host relations.—Eggs of *E. sylvestris* were found singly in the host larvae. When the host larvae were dissected, the parasitoid eggs and first instar larvae were found free-floating anywhere in the host body cavity. No attempts to parasitize the host eggs were recorded. Parasitoid larvae hatch about one day after being laid. Females of *E. sylvestris* oviposited into weevil larvae of various instars, but only second instar larvae of the parasitoid were found within the mature host larvae. Only one parasitoid larva per host larva was found in all studied samples. Parasitoid larvae could sometimes be observed while inside the host.

The larvae of *E. sylvestris* never emerged from the host's body within the pods of *S. loeselli*. Behaviour and pupation of parasitized host weevil larvae did not differ from unparasitized.

DISCUSSION

Life history of *Entedon sylvestris*

Females of *Entedon sylvestris* attack their hosts, the weevils *Ceutorhynchus sisymbrii*, at their larval stage. The larvae of *C. sisymbrii* feed on the seeds of the small tumbleweed mustard, *Sisymbrium loeselii* L., and leave the host plant's pod when mature. Unlike most other parasitoids of seed-feeding weevils, which finish their ontogenesis and kill the hosts inside the host plant pods (e.g. *Trichomalus* spp., *Mesopolobus* spp., *Necremnus* spp.), the larva of *E. sylvestris* is in its second instar when the the host larva leaves the pod. The

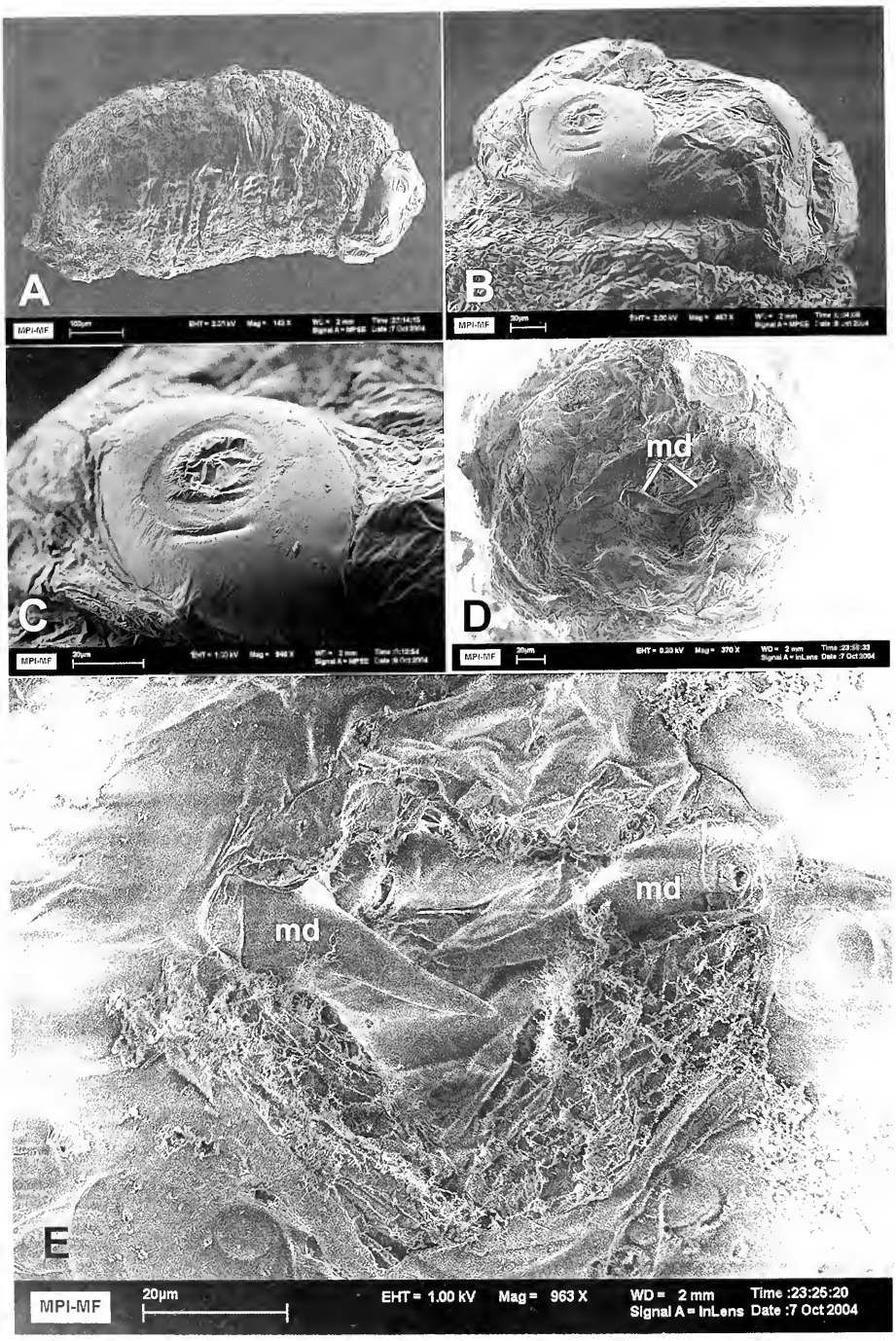

Fig. 10. A–E. *E. sylvestris*, final instar larva (isolated from the dead host larva): A, habitus, B, head, lateral view; C, antenna enlarged; D, head, frontal view; E, mandibles; ant, antenna; md, mandible.

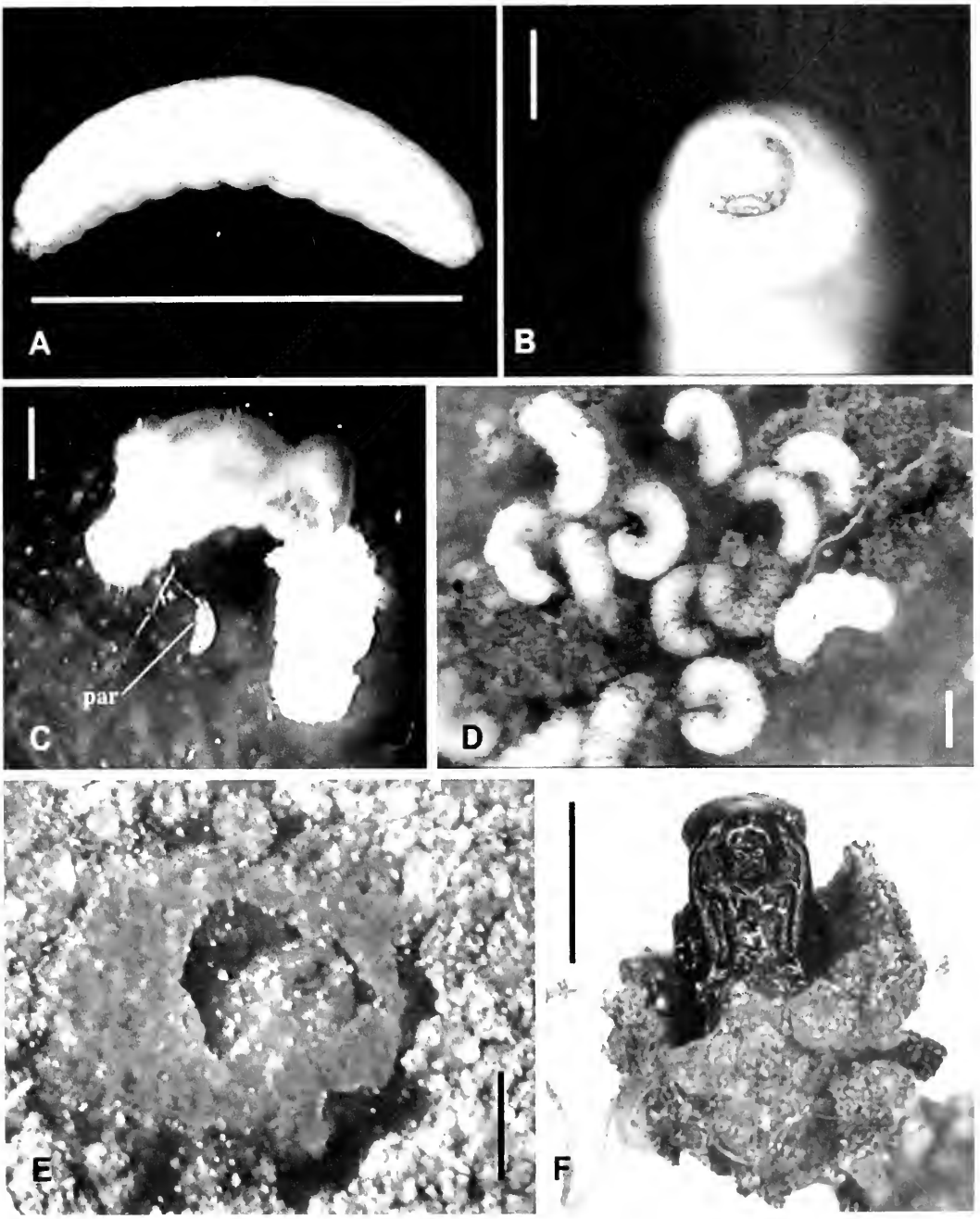

Fig. 11. A, B, the mature larva of *Ceutorhynchus sisymbrii*; C, first-instar larva of *E. sylvestris* isolated from the host's body; D, the dead weevil larvae isolated from the soil sample and treated by the lactic acid solution; E, the mature larva of *C. sisymbrii* creates an earthen cell (the larva is visible inside); F, the pupa of *E. sylvestris* in the host's earthen cell; par, parasitoid larva. Scale bars: A, 3 mm; B, 0.3 mm; C, 0.3 mm; D, E, F, 1 mm.

moult of the parasitoid larva into the final instar and final consumption of the host take place within the host's body, underground. Pupation takes place outside of the remnants of the host's body, also underground, at a depth of at least of 2–3 centimeters. The underground pupation means that adult parasitoids must penetrate at least 2 cm of soil to emerge the following spring.

Underground pupation is rather rare within Chalcidoidea, perhaps due to the small body size of these insects and corresponding problems with emergence from soil. Apart from *Entedon sylvestris*, the pupation and consequent emergence from the earthen cells of its host, is recorded for *E. cyanellus* Dalman, a parasitoid of *Tichius quinquepunctatus* (L.) (Gumovsky 1997). However, no detailed biological information is available for *E. cyanellus*, and records of its biology refer just to labels of museum specimens. So, *E. sylvestris* is the only chalcid species of known biology, which begins its ontogenesis above the ground and ends it underground.

Both known species for which underground pupation is known or suspected (*E. sylvestris*, *E. cyanellus*), have the produced anterior margin of the clypeus (Fig. 1, cly). The produced clypeus is diagnostic for the *cyanellus* and *costalis* groups of *Entedon* (Gumovsky 1997), and occasionally present in species of some other groups (*E. kerteszi* Erdös, *E. occidentalis* Girault, *E. diabolus* Rasplus). The function of the shape of the clypeus is unknown. The adult chalcids feed by sucking liquids through the use of their labio-maxillary complex. Neither the clypeus nor the mandibles are actively involved in this process. One of the possible functions of the produced clypeus may be associated with facilitating emergence from the ground. *Entedon rumicis*, *E. pharnus* and *E. philiscus* Walker also have the anterior margin of the clypeus produced, but their adults emerge from the host plant's stems, not soil (Fisher 1970). The anterior margin of the clypeus is less produced in these species than in *E. sylvestris* and *E. cyanellus*. Further observations on the emergence procedure may reveal other behavioral peculiarities and functional devices for the species of *Entedon* having an "underground span" in their life cycles.

Larval morphology

Beaver (1966) mentioned that the first-instar larva of *E. ergias* has 12 segments, but the last segment bears a dorsal plate with a series of sharp spines on its edge. Fisher (1970), when describing the first instar larva of *E. rumicis*, mentioned that it has the head capsule and 13 body segments, with "the last abdominal segment ventrally with a sclerotized plate with irregularly spinous edges". The same author also mentioned that the first-instar larvae of *E. pharnus* and *E. philiscus* have a similar body shape. Since the first-instar larvae of other species have 13 body segments, Beaver's statement of the possession of only 12 body segments by the first instar larva of *E. ergias* is likely erroneous.

The morphological peculiarities of the first-instar larva of *E. sylvestris* include the notable indentation on the XIII (last) body segment (Figs 6C, D, 8C, D). This indentation is likely equivalent to the plates with spinous edges reported for the first-instar larva of *E. ergias* (Beaver 1966) and *E. rumicis* (Fisher 1970), and also may be assumed for the larvae of *E. pharnus* and *E. philiscus* (mentioned as similar to the larva of *E. rumicis* by Fisher 1970). The tubercles of the indentation (the "caudal crown") is likely homologous to the small curved teeth of the dorsal semicircular serrations (Fig. 6C) along the anterior margins of the segments IV–XII. The function of the "caudal crown" for these larvae remains obscure, but there is no evidence of its usage for movement within the body cavity, since the parasitoid larvae observed within the host's body are generally passive.

The first-instar larva of *E. sylvestris* is, to some extent, similar to the larva of *Miscogaster* sp. described by Parker and Thomson (1925). Both larvae are apneustic, have the cuticular spines arranged in encircling lines (striations) on the body segments (IV–XII) and peculiar indentation of the last body segment (a semi-circular or bilobed "caudal crown"). However, the tubercles of the "caudal crown" are subequal in length in the larva of *E. sylvestris* (two inner spines are stouter than the surrounding spines of the "caudal crown" in *Miscogaster* sp.) and the sensorial structures of the head have a somewhat different arrangement.

Although data is available for only a few species, the "caudal crown" is likely inherent to all first instar larvae of *Entedon*. This character is quite remarkable and rare in Chalcidoidea (Parker and Thomson 1925), and thus may be used later to support monophyly of *Entedon*, if found in other species of the genus. Also, the combination of a nearly bare body and the "caudal crown" may facilitate separating the larvae of this genus from other endoparasitoid larvae. Furthermore, the proper affiliation of the first-instar larva of *E. sylvestris* to a peculiar larval type requires a revision of the current classification (Parker 1924) of these types in Chalcidoidea.

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Phylogenetic Analysis of *Chaenusa sensu lato* (Hymenoptera: Braconidae) using Mitochondrial NADH 1 Dehydrogenase Gene Sequences

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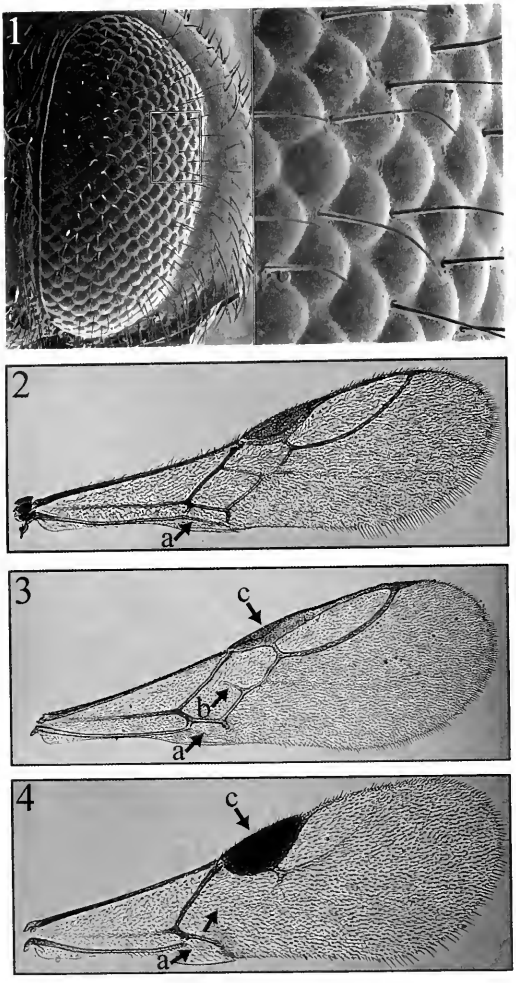
Abstract.—Alysiinae currently contains over 1,500 described species and is divided into the tribes Alysiini and Dacnusini. There is disagreement on how species should be grouped within Dacnusini, and *Chaenusa* Haliday is a prime example. *Chaenusa sensu lato* is defined by the presence of setae on the compound eyes (Griffiths 1964). Alternatively, Riegel (1950, 1982) treated *Chaenusa s.l.* as three genera, *Chaenusa sensu stricto*, *Chorebidea* Viereck, and *Chorebidella* Riegel, and differentiated the genera primarily using forewing venation and shape of the forewing stigma. Phylogenetic analyses using molecular data have not been undertaken. Therefore, we assessed the monophyly and interspecific relationships of *Chaenusa s.l.*, *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella* through maximum parsimony, maximum likelihood, and Bayesian analyses using mitochondrial NADH 1 dehydrogenase gene sequences. *Chaenusa s.l.* and *Chorebidea* were not monophyletic in any of the analyses, but four of five species of *Chorebidea* always formed a clade. Further, *Chaenusa s.s.* and *Chorebidella* were monophyletic in all analyses and were always sister taxa. The results of this study largely support Riegel's (1950, 1982) treatment of *Chaenusa s.l.* as *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella*. However, we suggest that *Chaenusa s.l.* be retained until additional phylogenetic analyses have been undertaken to confirm the relationships inferred in this study. In addition to the phylogenetic analyses, we discuss the morphological features relevant to Griffiths' definition of *Chaenusa s.l.* and Riegel's definition of *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella*.

Alysiinae currently contains over 1,500 described species, and estimates of global richness range from 2,900 to 5,300 species (Dolphin and Quicke 2001). The monophyly of Alysiinae is firmly established based on the possession of exodont mandibles and the complete loss of the occipital carina (Griffiths 1964, Shaw and Huddleston 1991, Wharton 1997). Host records suggest that all alysiines are koinobiont endoparasitoids of cyclorrhaphous Diptera (Shaw and Huddleston 1991, Wharton and Austin 1991, Wharton 1997).

Two tribes are currently recognized in Alysiinae: Alysiini and Dacnusini. Alysiini is probably nonmonophyletic as it is defined by the presence of forewing vein r-m (a plesiomorphy). Dacnusini is considered monophyletic based on the absence of forewing vein r-m (an apomorphy) (Griffiths 1964, Shaw and Huddleston 1991, Wharton 1994) and has consistently been recognized, although at different hierarchal levels, since Förster (1862). There is widespread disagreement on how species should be grouped within Dacnusini, and *Chaenusa* Haliday is a prime example. Nixon (1943) divided dacnusines with setiferous compound eyes (Fig. 1) into two genera, *Chaenusa* and *Chorebidea* Viereck, and differentiated the genera using forewing venation and shape of the forewing stigma. Riegel (1950) established *Chorebidella* Riegel, a third genus contain-



Figs 1–4. *Chaenusa sensu lato*, *Chaenusa sensu stricto*, *Chorebidea*, and *Chorebidella*. 1, *Chorebidea americana*, setiferous compound eyes. 2, *Cha. quadriceps*, 1st subdiscal cell closed. 3, *Chorebidea saxicola*, 1st subdiscal cell open, RS+M partially present, and stigma "long". 4, *Chaenusa* sp. 3, 1st subdiscal cell open, RS+M absent, and stigma "short, wide". a = 1st subdiscal cell, b = RS+M, and c = stigma.

ing dacnusines with setiferous eyes. Like Nixon (1943) Riegel (1950) differentiated the genera primarily using forewing venation and shape of the forewing stigma. Riegel (1950) regarded all dacnusines with setiferous eyes and a closed 1st subdiscal cell as *Chaenusa* (Fig. 2); he segregated dacnusines with setiferous eyes and an open 1st subdiscal cell into *Chorebidea* or *Chorebidella*. Species with forewing vein RS+M at least partially present and a "long" stigma were considered *Chorebidea* (Fig. 3); species with RS+M absent and a "short, wide" stigma were considered *Chorebidella* (Fig. 4). Griffiths (1964) hypothesized that all dacnusines with setiferous eyes form a monophyletic group and synonymized *Chaenusa sensu stricto*, *Chorebidea*, and *Chorebidella* (i.e., *Chaenusa sensu lato*). However, Riegel (1982) disagreed with Griffiths' synonymies and continued to treat *Chaenusa sensu* Griffiths (1964) as three genera. Riegel (1982), the only comprehensive treatment of North American species of *Chaenusa s.l.*, included several new species in *Chaenusa s.s.* and *Chorebidea*, but Wharton (1997) followed *Chaenusa sensu* Griffiths (1964) rather than *Chaenusa sensu* Riegel (1982).

With 29 described species worldwide, *Chaenusa s.l.* is small relative to other dacnusine genera (e.g., over 240 species of *Chorebus* Haliday). Nearly all species are Nearctic or Palaearctic, but three species are known from Australia, and one species each is known from Madagascar and Argentina. As far as is known, flies in the ephydrid genus *Hydrellia* Robineau-Desvoidy are exclusively utilized as hosts (Griffiths 1964, Shaw and Huddleston 1991, Wharton and Austin 1991, Wharton 1997). *Hydrellia* is an important group for classical biological control of aquatic weeds. For example, *Hydrellia pakistanae* Deonier and *Hydrellia balciunasi* Bock have been imported and released for control of *Hydrilla verticillata* (L.f.) Royle in the United States. However, *Hydrellia* also contains species that are rice pests, such as *Hydrellia griseola* (Fallén) and *Hydrellia philippina* Ferino. Species of *Chaenusa s.l.* may hinder classical biological control programs as contaminants in the quarantine phase (Wharton 1997) or through parasitism (by endemics) of introduced natural enemies. Conversely, species of *Chaenusa s.l.* may be important natural enemies of pest flies (Natarajan and Mathur 1980).

Table 1. Species analyzed in this study and their respective taxonomic placements, locality data, source repositories or collectors, and GenBank accession numbers. CNG = Cimarron National Grassland, KPBS = Konza Prairie Biological Station, and SFF = Santuario de Fauna y Flora.

Species	Taxonomic Placement	Locality	Source	Accession No.
Chaenusa n. sp. 1	*Chaenusa s.s.*	Chile: Isla Chiloé, Vilupulli	UCDC	DQ917269
Chaenusa quadriceps	*Chaenusa s.s.*	Canada: ON: Ottawa	TAMU	DQ917272
Chaenusa n. sp. 2	*Chorebidea*	U.S.A.: GA: Clarke Co., Athens	TAMU	DQ917270
Chaenusa n. sp. 3	*Chorebidea*	Colombia: Boyacá, SFF Iguaque	IAVH/HIC	DQ917271
Chorebidea americana	*Chorebidea*	U.S.A.: FL: Putnam Co., Rodman Reservoir	TAMU	DQ917276
Chaenusa sp. 1	*Chorebidea*	Canada: SK: ~35 km W. Rosthern	MJY	DQ917273
Chaenusa sp. 2	*Chorebidea*	U.S.A.: SC: Lexington Co., Lexington	CNC	DQ917274
Chaenusa bergi	*Chorebidella*	U.S.A.: KS: Riley Co., KPBS	RRK/GZ	DQ917268
Chaenusa sp. 3	*Chorebidella*	India: Karnataka, Bangalore, Kumbalgodu	TAMU	DQ917275
Chorebus sp. 1	*affinis* group	U.S.A.: AZ: Santa Cruz Co., Peña Blanca Lake	RRK	DQ917277
Chorebus sp. 2	*affinis* group	U.S.A.: AZ: Santa Cruz Co., Peña Blanca Lake	RRK	DQ917278
Coelinius ferruginea	*Coelinius s.l.* (*Lepton*)	U.S.A.: KS: Riley Co., KPBS	RRK/GZ	DQ917279
Coelinius hopkinsii	*Coelinius s.l.* (*Lepton*)	U.S.A.: KS: Riley Co., KPBS	RRK/GZ	DQ917280
Dapsilarthra sp. 1	*balteata* group	U.S.A.: TX: Brazos Co., Lick Creek Park	RRK	DQ917281
Opius sp. 1	Opiinae	U.S.A.: KS: Morton Co., CNG	RRK/GZ	DQ917282

The taxonomic history discussed above illustrates that the limits of *Chaenusa* are uncertain. The monophyly of *Chaenusa s.l.*, *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella* has never been assessed through phylogenetic analysis, and character systems other than morphology (e.g., DNA sequence data) have not been utilized. Resolving the taxonomic limits of *Chaenusa* and understanding the evolutionary relationships among species in the genus are important factors for predicting their potential as biological control antagonists or agents. Additionally, increased taxonomic stability facilitates revisionary work on a group. Smith et al. (1999) and Michel-Salzat and Whitfield (2004) demonstrated the utility of mitochondrial NADH 1 dehydrogenase (ND1) gene sequences for resolving evolutionary relationships among aphidiine and microgastrine braconids, respectively. Thus, the objective of this study was to assess the monophyly and interspecific relationships of *Chaenusa s.l.*, *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella* using ND1 gene sequences.

MATERIALS AND METHODS

Terminology.—Terminology for mandibular teeth and external male genitalia follows Wharton (1977). Terminology for all other anatomical features, including wing cells and veins, follows Sharkey and Wharton (1997). Abbreviations for repositories are as in Evenhuis and Samuelson (2005).

Taxon sampling.—Species analyzed in this study and their respective taxonomic placements, locality data, source repositories or collectors, and GenBank accession numbers (DQ917268–DQ917282) are listed in Table 1. Specimens used for DNA isolations were acquired from repositories as indicated in Table 1 or were collected by RRK, GZ, and Matthew J. Yoder (MJY, Texas A&M University) using yellow pan traps, sweep nets, and Malaise traps. Voucher specimens for each species are deposited in the Ambrose Morell Collection for Molecular and Microbial Research at the American Museum of Natural History. With the exception of *Chaenusa pallidinervis* (Brèthes), holotypes were examined for all described alysiines dis-

cussed in this paper. The holotype of *Gyrocampa pallidinervis* Brèthes is housed in the Museo Argentina de Ciencias Naturales (MACN). The first author made multiple requests, but the MACN did not loan the holotype.

The ingroup was composed of either 13 species of Dacnusini or 13 species of Dacnusini and one species of Alysiini depending on the analysis. Nine species of *Chaenusa s.l.* were included, with *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella* represented by two, five, and two species, respectively. Undescribed species were considered *Chaenusa s.s.*, *Chorebidea*, or *Chorebidella* based on forewing configuration. *Chaenusa* n. sp. 1–3 will be described in a taxonomic revision of New World *Chaenusa s.l.* (Kula in preparation). *Chaenusa* sp. 1 and 2 appear to be undescribed species but are only known from one and two individuals, respectively. Thus, RRK awaits the discovery of additional specimens before describing them. Evaluation of the literature for Old World *Chaenusa s.l.* suggests that *Chaenusa* sp. 3 is also undescribed.

Two species each from *Chorebus* and *Coelinius* Nees were also treated as ingroup taxa to test the monophyly of *Chaenusa s.l.* Species of *Chorebus* and *Coelinius* possess morphological features (i.e., eye setation, number and position of mandibular teeth, metapleural setation, metasomal compression) that suggest the potential for a close relationship with certain species of *Chaenusa s.l.* (Kula personal observation). Both species of *Chorebus* fit in the *affinis* group (Griffiths 1968), and both species of *Coelinius* fit the concept of *Lepton* Zetterstedt (=*Coelinidea* Viereck) in Griffiths (1964) (as a subgenus) and Riegel (1982) (as a genus).

A species of either *Opius* Wesmael or *Dapsilarthra* Förster was specified as the outgroup to root trees depending on the analysis. Previous phylogenetic analyses support a sister group relationship between Alysiinae and Opiinae (Quicke and van Achterberg 1990, Wharton et al. 1992, Quicke 1994, Belshaw et al. 1998, Dowton et al. 1998, Shi et al. 2005). Griffiths (1964) suggested that species of *Dapsilarthra* (Alysiini) and Dacnusini might be closely related based on parasitism of leaf-mining agromyzids. Species of *Dapsilarthra* almost exclusively attack leaf-mining agromyzids (Wharton 1984, 1997), and dacnusines that Griffiths (1964) considered morphologically plesiomorphic are parasitoids of leaf-mining agromyzids. In analyses with *Opius* sp. 1 used to root trees, *Dapsilarthra* sp. 1 was included in the ingroup to explore the monophyly of Dacnusini. *Dapsilarthra* sp. 1 was used to root trees in analyses that excluded *Opius* sp. 1.

DNA isolation, amplification, sequencing, and alignment.—Genomic DNA was isolated from individual wasps using a DNeasy® Tissue Kit (Qiagen) according to the manufacturer's protocol for insects. Most specimens were ethanol-preserved, but several were dried, pinned specimens up to 14 years old. Polymerase chain reaction (PCR) amplifications and sequencing reactions were performed using an MJ Research PTC-200 thermal cycler. A portion of the ND1 gene was amplified using PCR set up in 25 µl volume. Oligonucleotide primers (ND1F: 5′-GATAAATCAAAWGGKGT-3′, ND1R: 5′-CAACCTTTTAGTGATGC-3′) and the PCR program were as in Smith et al. (1999) except the annealing temperature was optimized at 47 °C. PCR products were purified using a Qiaquick® PCR Purification Kit (Qiagen) according to the manufacturer's protocol. Both strands of all purified PCR products were sequenced using the PCR primers as sequencing primers. Sequencing reactions were performed in 10 µl volume using an ABI Prism® BigDye™ Terminator v3.0 Ready Reaction Cycle Sequencing Kit (Applied Biosystems) according to the manufacturer's protocol. Sequencing reaction products were purified using spin columns filled with Sephadex® (Amersham Biosciences), dehydrated by vacuum centrifuge, and sent to the DNA Sequenc-

ing & Synthesis Facility at Iowa State University for gel runs on an ABI Prism® 3700 DNA Analyzer (Applied Biosystems). Sequences generated from the forward and reverse primers were aligned and edited in Sequencher™ 4.1.2 (Gene Codes Corporation) to acquire a consensus sequence for each species. Consensus sequences were manually aligned in SeqPup 0.6 (Gilbert 1996) to produce a DNA sequence data matrix. The DNA data matrix was translated to construct an amino acid (AA) sequence data matrix using the *Drosophila* Fallén mtDNA genetic code in MacClade 4.06 (Maddison and Maddison 2003).

DNA and AA sequence characteristics and phylogenetic analysis.—The number of constant, variable parsimony uninformative, and parsimony informative characters were determined using PAUP* 4.0b10 (Swofford 2002), as were mean base frequencies. PAUP* 4.0b10 was also used to test for significant heterogeneity of base frequencies across taxa; base frequencies were considered significantly heterogeneous if $P \leq 0.05$.

Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed using PAUP* 4.0b10. Maximum parsimony analyses were conducted for the DNA and AA data matrices using the branch and bound algorithm. Modeltest 3.06 (Posada and Crandall 1998) was used to determine the model of molecular evolution that best fit the data, and subsequently, ML analyses were conducted for the DNA data matrix using the heuristic search option with stepwise addition, 100 random addition sequence replicates, and tree bisection-reconnection (TBR) branch swapping. If the Hierarchical Likelihood Ratio Test (hLRT) and the Akaike Information Criterion (AIC) in Modeltest selected different models, ML analyses were performed using each model. Support for individual clades was assessed via bootstrap analyses. For MP 1,000 pseudoreplicates with the branch and bound algorithm were used. For ML 100 pseudoreplicates using the heuristic search option with stepwise addition, 50 random addition sequence replicates, and TBR branch swapping were used.

Bayesian analyses were performed using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001). Modeltest 3.06 was used to determine the model of molecular evolution that best fit the data, and subsequently, Bayesian analyses were performed for the DNA data matrix. The data matrix was partitioned by codon position (i.e., 1st, 2nd, 3rd), and among-site rate variation was set (as a prior) to allow variable rates across partitions. The model of nucleotide substitution and among-site rate variation was set as determined using Modeltest. The following model parameters were unlinked across the partitions: substitution rates of GTR model, character state frequencies, gamma shape parameter, and proportion of invariable sites. Each run consisted of 1,000,000 generations with a random starting tree and sample frequency of every 100 generations. The burnin was determined by constructing an XY scatter plot (i.e., generation × log likelihood value) using Microsoft® Excel to determine the number of generations until log likelihood values stabilized. Trees sampled prior to the generation at which log likelihood values stabilized were not included in the consensus tree. A 50% majority-rule consensus of the retained trees, showing the frequency of all observed bipartitions (i.e., posterior probabilities), was constructed using PAUP* 4.0b10.

Maximum parsimony analyses with *Chaenusa s.l.* constrained as monophyletic were also performed for the DNA data matrix. The search parameters were the same as for unconstrained MP analyses as discussed above. Most parsimonious trees (MPTs) from unconstrained and constrained analyses were compared statistically using the "Compare-2" permutation test (Faith 1991) in PAUP* 4.0b10. Under MP each of 10,000 random matrices (with

Table 2. Number of constant (C), variable parsimony uninformative (VPU), and parsimony informative (PI) characters for all nucleotide (nuc) and amino acid (AA) sites and positions (Pos) 1, 2, and 3 with *Opius* sp. 1 excluded (excl) and included (incl).

Dataset	C	VPU	PI
All nuc sites (*Opius* sp. 1 excl)	241	66	123
All nuc sites (*Opius* sp. 1 incl)	234	60	136
Pos 1 (*Opius* sp. 1 excl)	83	26	34
Pos 1 (*Opius* sp. 1 incl)	81	25	37
Pos 2 (*Opius* sp. 1 excl)	119	7	17
Pos 2 (*Opius* sp. 1 incl)	116	8	19
Pos 3 (*Opius* sp. 1 excl)	39	33	72
Pos 3 (*Opius* sp. 1 incl)	37	27	80
All AA sites (*Opius* sp. 1 excl)	79	24	40
All AA sites (*Opius* sp. 1 incl)	74	26	43

all taxa randomized) were analyzed using the heuristic search option with stepwise addition, 500 random addition sequence replicates, and TBR branch swapping. The length difference between two trees (i.e., alternative hypotheses of relationships) was considered significant if $P \leq 0.05$.

RESULTS

DNA and AA sequence characteristics.—After sequence editing the aligned DNA data matrix was 430 bp and included no gaps. The DNA data matrix translated to an AA data matrix of 143 AAs. The number of constant, variable parsimony uninformative, and parsimony informative characters for all sites and positions 1, 2, and 3 with *Opius* sp. 1 excluded and included are reported in Table 2.

Evaluation of the mean base frequencies revealed a high A+T nucleotide bias, particularly in the first and third positions (Table 3). However, significant heterogeneity of base frequencies across taxa was detected only for position 3 when *Opius* sp. 1 was included (Table 4). High A+T nucleotide bias and less constrained nucleotide change relative to positions 1 and 2 may cause a high level of homoplasy in position 3 of insect mitochondrial protein-coding genes. Therefore, MP and bootstrap analyses were performed, as described above, with *Opius* sp. 1 included and position 3 excluded.

In Modeltest the hLRT selected the TIM model with a proportion of invariable sites and gamma distributed rate variation among sites; the AIC selected the TrN model with a proportion of invariable sites and gamma distributed rate variation among sites. Maximum likelihood analyses using each model resulted in trees with identical topologies, and the results of analyses using the TrN model are presented below.

Phylogenetic analysis.—Maximum parsimony analysis of the DNA data matrix with *Opius* sp. 1 excluded resulted in two MPTs (tree length = 387 steps, consistency index excluding uninformative characters (CI) = 0.5609, retention index (RI) = 0.5959) (Fig. 5). The trees differed only in the placement of *Chaenusa* n. sp. 3 as either sister to *Chorebus* sp. 1 or sister to the rest of the ingroup. *Chaenusa s.l.* was not mono-

Table 3. Mean base frequencies for all sites and positions (Pos) 1, 2, and 3 with *Opius* sp. 1 excluded (excl) and included (incl).

Dataset	A	C	G	T
All sites (*Opius* sp. 1 excl)	0.35626	0.10279	0.07695	0.46401
All sites (*Opius* sp. 1 incl)	0.35709	0.10381	0.07671	0.46239
Pos 1 (*Opius* sp. 1 excl)	0.35317	0.07908	0.09507	0.47267
Pos 1 (*Opius* sp. 1 incl)	0.35514	0.07901	0.09441	0.47144
Pos 2 (*Opius* sp. 1 excl)	0.20829	0.18746	0.11588	0.48836
Pos 2 (*Opius* sp. 1 incl)	0.20812	0.18726	0.11619	0.48843
Pos 3 (*Opius* sp. 1 excl)	0.50735	0.04165	0.02022	0.43078
Pos 3 (*Opius* sp. 1 incl)	0.50803	0.04496	0.01983	0.42719

Table 4. Results of tests for significant heterogeneity of base frequencies across taxa for all sites and positions (Pos) 1, 2, and 3 with *Opius* sp. 1 excluded (excl) and included (incl).

Dataset	χ^2	*P*
All sites (*Opius* sp. 1 excl)	17.509269	0.99882241
All sites (*Opius* sp. 1 incl)	19.096701	0.99908575
Pos 1 (*Opius* sp. 1 excl)	12.619144	0.99998081
Pos 1 (*Opius* sp. 1 incl)	13.202722	0.99999385
Pos 2 (*Opius* sp. 1 excl)	2.302238	1.00000000
Pos 2 (*Opius* sp. 1 incl)	2.338632	1.00000000
Pos 3 (*Opius* sp. 1 excl)	53.386385	0.06219822
Pos 3 (*Opius* sp. 1 incl)	60.168328	0.03417160

phyletic. In both trees the *Coelinius* clade was sister to the clade formed by four of the five species of *Chorebidea* included in the analysis. Further, *Chaenusa* n. sp. 3 either formed a clade with *Chorebus* sp. 1 and *Chorebus* sp. 2 or was sister to the rest of the ingroup. *Chorebidea* was not monophyletic, although four of five species of *Chorebidea* included in the analysis formed a clade with 94% bootstrap support. *Chorebus* was monophyletic in one tree, but bootstrap support was <50%. *Chaenusa s.s.*, *Chorebidella*, and *Coelinius* were monophyletic with 97%, 100%, and 75% bootstrap support, respectively. Bootstrap support for the relationships among these clades was <50% except for the sister group relationship between *Chaenusa s.s.* and *Chorebidella* (99% bootstrap support).

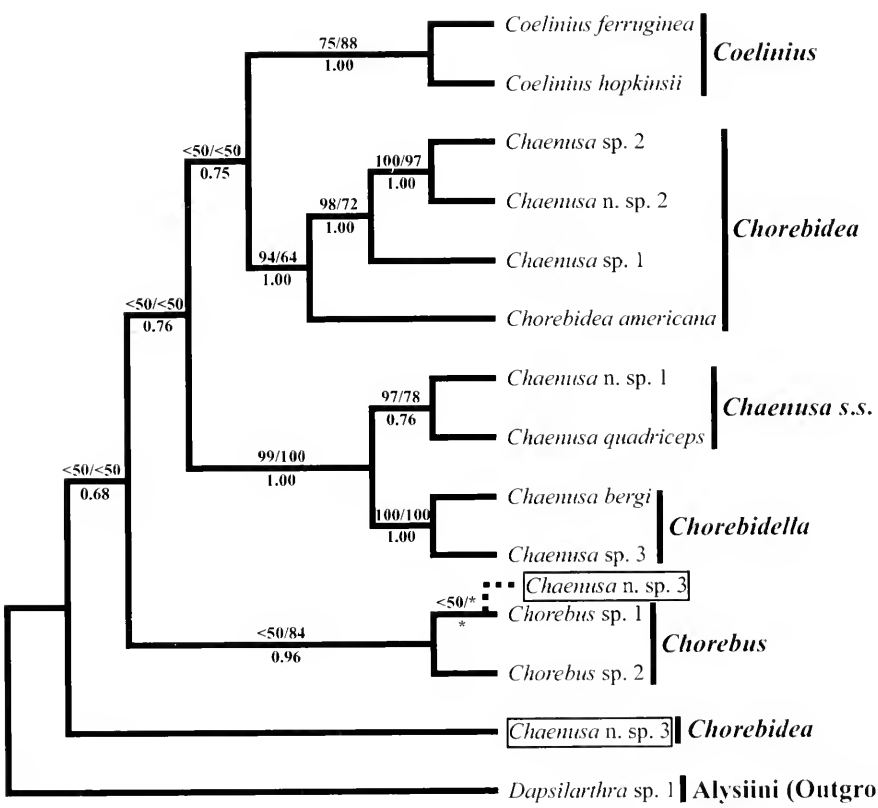


Fig. 5. Composite cladogram of two most parsimonious trees resulting from maximum parsimony analysis of the DNA data matrix with *Opius* sp. 1 excluded. Dashed line indicates alternative placement of *Chaenusa* n. sp. 3. Maximum parsimony bootstrap values are above branches and left of slashes. Where clades were recovered in maximum likelihood (ML) analysis with *Opius* sp. 1 excluded, bootstrap values are above branches and right of slashes. Where clades were recovered in Bayesian analysis with *Opius* sp. 1 excluded, posterior probabilities are below branches. Asterisks above and below branches indicate clades not recovered in ML and Bayesian analysis, respectively.

Table 5. Bootstrap support and posterior probabilities for groups within Dacnusini recovered through maximum parsimony (MP) and Bayesian analyses with *Opius* sp. 1 included. Maximum parsimony analyses were conducted with position (Pos) 3 included (incl) and excluded (excl). nr = groups not recovered.

Group	MP (Pos 3 incl)	MP (Pos 3 excl)	Bayesian
Chaenusa s.s.	97	100	0.77
Chorebidella	100	99	1.00
4 of 5 *Chorebidea*	98	85	1.00
Chaenusa s.s. + *Chorebidella*	99	81	1.00
Chorebus	nr	nr	0.88
Coelinius	67	67	1.00
Chorebus sp. 1 + *Chaenusa* n. sp. 3	59	<50	nr
Chorebus + *Chaenusa* n. sp. 3	62	<50	0.84

Maximum likelihood and Bayesian analyses of the DNA data matrix with *Opius* sp. 1 excluded resulted in a most likely tree (-Ln likelihood value = 2246.66073) and a 50% majority-rule consensus tree, respectively, with topologies identical to the MP tree with *Chaenusa* n. sp. 3 sister to the rest of the ingroup (Fig. 5). For the Bayesian consensus tree, the burnin was the first 50 trees. Bootstrap support for ML and posterior probabilities for Bayesian are reported in Fig. 5.

Maximum parsimony analysis with *Opius* sp. 1 included resulted in a single MPT (tree length = 435 steps, CI = 0.5474, RI = 0.5729) (tree not shown). Dacnusini was monophyletic with 78% bootstrap support. The relationships among dacnusines were identical to the MP tree with *Opius* sp. 1 excluded and *Chaenusa* n. sp. 3 sister to *Chorebus* sp. 1 (Fig. 5). Analysis with position 3 excluded resulted in a single MPT (tree length = 177, CI = 0.5755, RI = 0.6118) (tree not shown) with a topology identical to the tree with position 3 included. Dacnusini was monophyletic, but bootstrap support was <50%. Bootstrap support for groups within Dacnusini for analyses with position 3 included and excluded are presented in Table 5.

Bayesian analysis of the DNA data matrix with *Opius* sp. 1 included resulted in a 50% majority-rule consensus tree (tree not shown) with a topology nearly identical to the MP tree with *Opius* sp. 1 excluded and *Chaenusa* n. sp. 3 sister to *Chorebus* sp. 1 (Fig. 5). The burnin was the first 70 trees. In terms of the relationships among dacnusines, the only differences between the trees were (1) *Chorebus* was monophyletic with *Chaenusa* n. sp. 3 sister to the *Chorebus* clade and (2) the clade containing all dacnusines except *Chaenusa* n. sp. 3, *Chorebus* sp. 1, and *Chorebus* sp. 2 was not recovered. Dacnusini was monophyletic with a posterior probability of 0.99. Posterior probabilities for groups within Dacnusini are presented in Table 5.

Maximum likelihood analysis of the DNA data matrix with *Opius* sp. 1 included resulted in a most likely tree (−Ln likelihood value = 2437.12877) with a topology considerably different than trees from all other analyses (Fig. 6). Dacnusini was not monophyletic. Rather, *Dapsilarthra* sp. 1 was sister to *Chaenusa* n. sp. 3, but bootstrap support for this relationship was <50%. *Chaenusa s.l.* was not monophyletic. *Chorebidea* was not monophyletic, although four of five species of *Chorebidea* included in the analysis formed a clade with 67% bootstrap support. *Chaenusa s.s.*, *Chorebidella*, *Chorebus*, and *Coelinius* were monophyletic with 75%, 99%, 80%, and 71% bootstrap support, respectively. Bootstrap support for the relationships among these clades was <50% except for the sister group relationship between *Chaenusa s.s.* and *Chorebidella* (98% bootstrap support).

Maximum parsimony analysis with *Opius* sp. 1 excluded and *Chaenusa s.l.* constrained as monophyletic resulted in two MPTs (tree length = 393 steps, CI = 0.5503, RI = 0.5782) (trees not shown) six steps longer than the MPTs from the unconstrained analysis. The "Compare-2" test revealed that the two MPTs from the

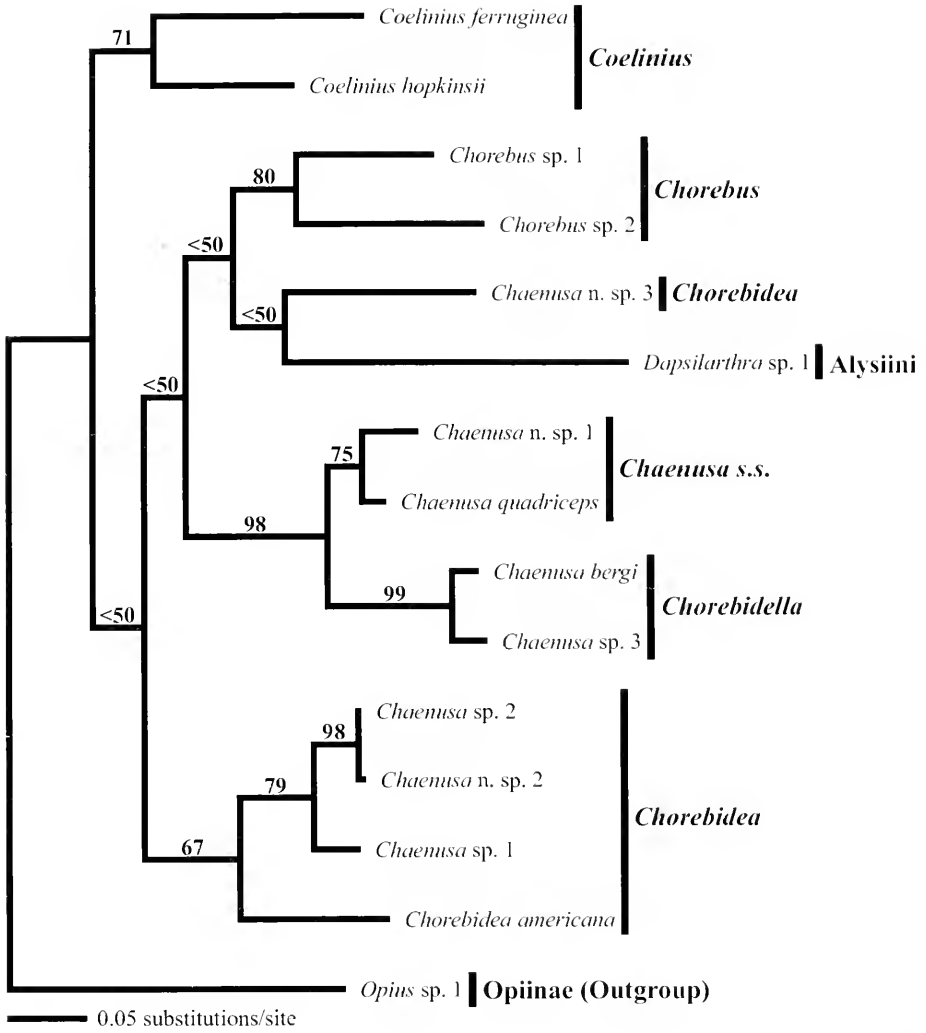


Fig. 6. Phylogram resulting from maximum likelihood analysis of the DNA data matrix with *Opius* sp. 1 included. Bootstrap values are above branches.

unconstrained analysis are not significantly shorter than either of the two MPTs from the constrained analysis (P = 0.125100, 0.127600, 0.162700, 0.165300). Maximum parsimony analysis with *Opius* sp. 1 included and *Chaenusa s.l.* constrained as monophyletic resulted in one MPT (tree length = 444 steps, CI = 0.5344, RI = 0.5499) (tree not shown) nine steps longer than the MPT from the unconstrained analysis. The "Compare-2" test revealed that the MPT from the unconstrained analysis is significantly shorter than the MPT from the constrained analysis (P = 0.031300).

Maximum parsimony analysis of the AA data matrix with *Opius* sp. 1 included resulted in two MPTs (tree length = 161 steps, CI = 0.7087, RI = 0.7176). Dacnusini was not monophyletic in the strict consensus of the two MPTs (Fig. 7). Rather, *Dapsilarthra* sp. 1 was sister to *Chaenusa* n. sp. 3, but bootstrap support for this relationship was <50%. *Chaenusa s.l.* was not monophyletic. *Chorebidea* was not monophyletic, although four of five species of

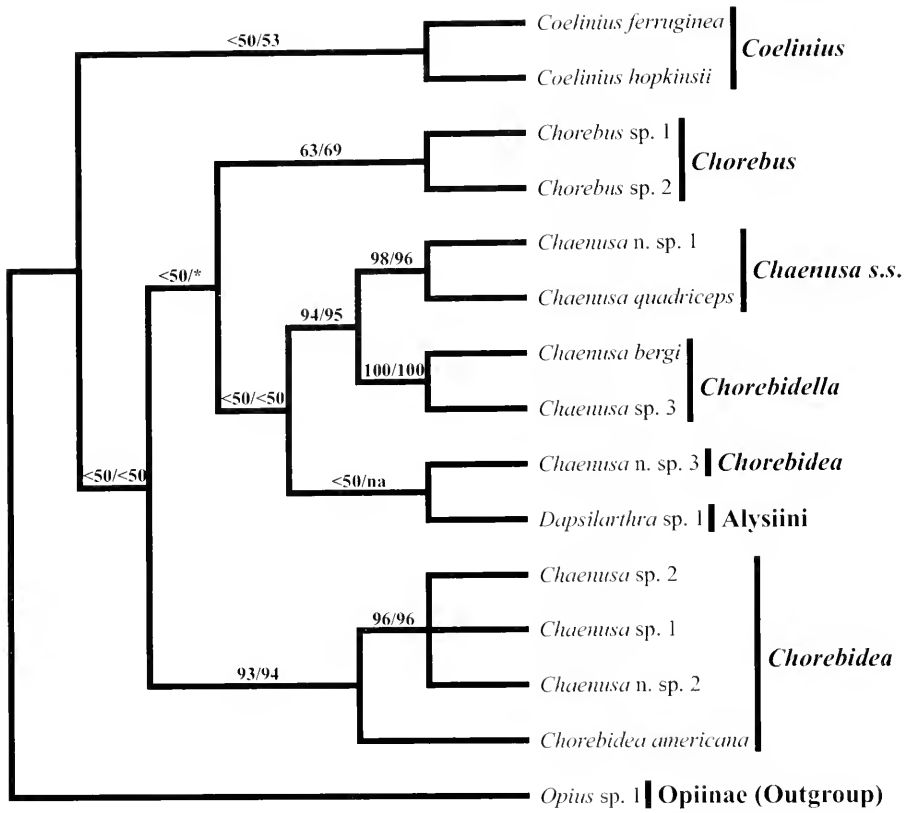


Fig. 7. Strict consensus of two most parsimonious trees resulting from maximum parsimony (MP) analysis of the amino acid data matrix with *Opius* sp. 1 included. Maximum parsimony bootstrap values are above branches and left of slashes. Where clades were recovered in MP analysis with *Opius* sp. 1 excluded, bootstrap values are above branches and right of slashes. The asterisk indicates a clade not recovered in MP analysis with *Opius* sp. 1 excluded. na = not applicable.

Chorebidea included in the analysis formed a clade with 93% bootstrap support. *Chaenusa s.s.*, *Chorebidella*, and *Chorebus* were monophyletic with bootstrap support of 98%, 100%, and 63%, respectively. *Coelinius* was monophyletic, but bootstrap support was <50%. Bootstrap support for the relationships among these clades was <50% except for the sister group relationship between *Chaenusa s.s.* and *Chorebidella* (94% bootstrap support).

Maximum parsimony analysis of the AA data matrix with *Opius* sp. 1 excluded resulted in six MPTs (tree length = 142 steps, CI = 0.7273, RI = 0.7479). In terms of the relationships among dacnusines, the strict consensus of the six MPTs (tree not shown) was identical to the strict consensus tree in Fig. 7 except the monophyly of *Chaenusa s.l.* was unresolved (see asterisk in Fig. 7). Bootstrap support is reported in Fig. 7.

DISCUSSION

DNA sequence characteristics.—Characteristics of the ND1 DNA sequences in this study are consistent with ND1 DNA sequences of other braconids (e.g., Smith and Kambhampati 1999, Smith et al. 1999, Michel-Salzat and Whitfield 2004). As in the aforementioned studies, the sequenced fragments in this study (including *Opius* sp. 1) are biased towards adenine (35.7%) and thymine (46.2%), particularly in the first (82.7%) and third (93.5%) positions. Significant heterogeneity of base frequen-

cies was detected for position 3 when *Opius* sp. 1 was included. As mentioned in Michel-Salzat and Whitfield (2004), the A+T nucleotide bias observed for insect mitochondrial DNA could influence the level of homoplasy, particularly in the first and third positions. However, 27.2% and 58.8% of the parsimony informative characters in the DNA data matrix with *Opius* sp. 1 included are in the first and third positions, respectively. Therefore, for most analyses all positions were considered and were not differentially weighted. We performed MP and bootstrap analyses with *Opius* sp. 1 included and position 3 excluded to examine the influence of position 3 on tree topology and branch support. The exclusion of position 3 had no influence on tree topology but resulted in lower bootstrap support for several clades. Conversely, there was a slight increase in CI and RI values when position 3 was excluded. This suggests that position 3 contains phylogenetic information that supports several clades but also increases the level of homoplasy in the data matrix.

Tribe Dacnusini.—Griffiths (1964) and Wharton (1994) suggested that Dacnusini is monophyletic based on the absence of forewing vein r-m. Further, Dacnusini is homogeneous in terms of host utilization; the tribe exclusively contains parasitoids of plant-mining flies, particularly parasitoids of leaf- and stem-mining agromyzids, chloropids, and ephydrids (Wharton 1997). Maximum parsimony, ML, and Bayesian analyses were conducted with *Dapsilarthra* sp. 1 included in the ingroup to explore the monophyly of Dacnusini. In MP and Bayesian analyses of the DNA data matrix, Dacnusini was monophyletic with 78% bootstrap support and a posterior probability of 0.99, respectively. However, neither ML analysis of the DNA data matrix nor MP analysis of the AA data matrix recovered Dacnusini. Rather, *Dapsilarthra* sp. 1 was always sister to *Chaenusa* n. sp. 3, but bootstrap support for this relationship was <50%. In MP analysis of the AA data matrix with *Chaenusa* n. sp. 3 excluded, Dacnusini was monophyletic in two of six MPTs, but bootstrap support was <50% (results not presented). Dacnusini was not monophyletic in ML analysis of the DNA data matrix with *Chaenusa* n. sp. 3 excluded (results not presented). Thus, ND1 DNA sequences and the absence of forewing vein r-m largely, but not conclusively, support the monophyly of Dacnusini. Exclusive utilization of plant-mining flies as hosts, particularly leaf- and stem-mining agromyzids, chloropids, and ephydrids (i.e., biological homogeneity), provides further indication that Dacnusini is monophyletic. However, more extensive taxon sampling and the use of additional markers more conserved than ND1 are needed to confirm the monophyly of Dacnusini and resolve the more ancient divergences within the tribe.

Genus Chaenusa sensu lato.—*Chaenusa s.l.* was not monophyletic in any of the analyses. Rather, the results indicate that certain species of *Chaenusa s.l.* are more closely related to species of *Chorebus* and *Coelinius* than they are to other species of *Chaenusa s.l.* This result is not surprising for several reasons. Certain species of *Chaenusa s.l.* possess morphological features that suggest the potential for a close relationship with species of *Chorebus* and *Coelinius*. As is observed for species of the *Chorebus affinis* group (Griffiths 1968), several species of *Chaenusa s.l.* have four-toothed mandibles with three major teeth and one small tooth along the ventral margin of elongate tooth 2. In this study *Chaenusa* n. sp. 3, *Chaenusa* n. sp. 1, and *Cha. quadriceps* (Ashmead) exhibit this condition, as do four described (i.e., *Chaenusa anticostae* Riegel, *Chaenusa californica* Riegel, *Chaenusa illinae* Riegel, *Chaenusa rossi* Riegel) and two undescribed Nearctic species of *Chaenusa s.l.* not included in this study (Kula unpublished). Further, the metapleural setation of *Chaenusa* n. sp. 3 is nearly oriented in a rosette surrounding a raised swelling, a character state used to

define *Chorebus*. *Chaenusa* n. sp. 3 forms a clade with *Chorebus* in certain MP and Bayesian analyses, and it is possible that *Chaenusa* n. sp. 3 is a species of *Chorebus* with setiferous eyes.

A character state in females of *Coelinius* is lateral compression of the metasoma. Females of *Chorebidea americana* Riegel, *Chorebidea bessae* Riegel, *Chorebidea mcclurei* Riegel, *Cha. rossi*, *Chorebidea saxicola* Riegel, and one undescribed Nearctic species of *Chaenusa s.l.* have a laterally compressed metasoma (Kula unpublished). In this study only *Chorebidea americana* clearly exhibits this condition. Further, *Coelinius* is partially defined on the possession of four-toothed mandibles with three major teeth and one small tooth between tooth 1 and 2. In this study *Chaenusa* sp. 2, *Chaenusa* n. sp. 2, and *Chaenusa* sp. 1 exhibit this condition, and it also occurs in an undescribed Nearctic species of *Chaenusa s.l.* not included in this study (Kula unpublished).

Griffiths (1964) proposed that among dacnusines setiferous eyes is unique to species of *Chaenusa s.l.* and is a synapomorphy that defines *Chaenusa s.l.* However, dacnusines in genera other than *Chaenusa s.l.* have setiferous eyes. New World species of *Chorebus* (47 morphospecies), *Coelinius* (19 morphospecies), *Coloneura* Förster (two morphospecies), *Dacnusa* Haliday (18 morphospecies), *Epimicta* Förster (two morphospecies), *Exotela* Förster (14 morphospecies), *Laotris* Nixon (six specimens), and *Synelix* Förster (one morphospecies) all have setiferous eyes. Only New World species of *Symphya* Förster (13 morphospecies) have glabrous eyes (Kula unpublished). Character states other than setiferous eyes clearly place the aforementioned species in their respective genera. In most cases the setae are straight and are so minute that they could easily escape detection using a stereomicroscope at 120× magnification (i.e., usually shorter than a facet width). For species of *Chaenusa s.l.*, at least some setae on the eyes are conspicuously longer than a facet width and are curved. However, 8.5% of the *Chorebus* and 5.3% of the *Coelinius* morphospecies examined have curved setae on the eyes longer than a facet width. Thus, the mere presence of setae on the eyes cannot be regarded as a synapomorphy that defines *Chaenusa s.l.*

Genus Chaenusa sensu stricto.—*Chaenusa s.s.* was monophyletic in all analyses, and branch support was moderate to strong. *Chaenusa s.s.* should be more extensively sampled in future phylogenetic analyses to provide a more robust assessment of monophyly. Six of the 11 described New World species of *Chaenusa s.l.* fit in *Chaenusa s.s.* (i.e., *Cha. anticostae*, *Cha. californica*, *Cha. illinae*, *Cha. pallidinervis*, *Cha. quadriceps*, *Cha. rossi*). However, all except *Cha. quadriceps* are only known from the holotype. Thus, a very small number of New World specimens of *Chaenusa s.s.* are available for DNA sequencing. Extensive collecting will be needed to increase the representation of New World *Chaenusa s.s.* in future phylogenetic analyses. The most successful methods for collecting specimens of *Chaenusa s.l.* are yellow pan traps placed along the shore of permanent lakes, ponds, and streams and sweeping within and along the edge of aquatic habitats.

Riegel (1950, 1982) defined *Chaenusa s.s.* using the following features: (1) 1st subdiscal cell closed, (2) stigma "short, wide", and (3) labial palpi four-segmented. Both species of *Chaenusa s.s.* included in this study have the 1st subdiscal cell closed, a relatively broad stigma, and three- or four-segmented labial palpi. The length of the distal palpomere in specimens with three-segmented labial palpi is approximately the combined length of palpomeres 3 and 4 in specimens with four-segmented labial palpi. Further, examination with a scanning electron microscope revealed that the distinction between palpomeres 3 and 4 is extremely weak in some specimens of *Chaenusa* n. sp. 1, *Cha. quadriceps*, and an

undescribed Nearctic species that fits *Chaenusa s.s.* Thus, it appears that three-segmented labial palpi in *Chaenusa* n. sp. 1 and *Cha. quadriceps* resulted from the fusion of palpomeres 3 and 4 or the division of palpomere 3 into two palpomeres.

Genus Chorebidea.—*Chorebidea* was not monophyletic in any of the analyses. However, four of five species of *Chorebidea* included in this study formed a clade in all analyses, and branch support was weak to strong. Riegel (1950, 1982) defined *Chorebidea* using the following features: (1) 1st subdiscal cell open, (2) forewing vein RS+M at least partially present, (3) stigma "long", (4) labial palpi three-segmented, and (5) gonoforceps "stocking-shaped in lateral view". All species of *Chorebidea* included in this study have an open 1st subdiscal cell through the partial or complete absence of forewing veins 2-1A and 2cu-a, and forewing vein RS+M is at least partially present. Both features exhibit some degree of intraspecific variation. The 1st subdiscal cell is rarely (3.1%, one of 32 specimens examined) closed in *Chaenusa* n. sp. 3, and although forewing vein RS+M is present for all species, it may vary from complete and tubular to minutely present posteriorly. Riegel (1950, 1982) included a "long" stigma in his concept of *Chorebidea*, but *Chorebidea americana* and *Chorebidea bessae* have a relatively broad stigma. The stigma is relatively long for *Chaenusa* sp. 2, *Chaenusa* n. sp. 2, *Chaenusa* sp. 1, and *Chaenusa* n. sp. 3 but is relatively broad for *Chorebidea americana*. *Chaenusa* sp. 2, *Chaenusa* n. sp. 2, *Chaenusa* sp. 1, and *Chorebidea americana* have three-segmented labial palpi, but the labial palpi are four-segmented for *Chaenusa* n. sp. 3. Lastly, *Chorebidea americana* has "stocking-shaped" gonoforceps, but *Chaenusa* sp. 2, *Chaenusa* n. sp. 2, and *Chaenusa* sp. 1 have gonoforceps that gradually narrow proximally to distally and are roughly triangular-shaped. *Chaenusa* n. sp. 3 has roughly rectangular-shaped gonoforceps that are truncate distally.

Genus Chorebidella.—*Chorebidella* was monophyletic in all analyses, and branch support was strong. *Chorebidella* should be more extensively sampled in future phylogenetic analyses to provide a more robust assessment of monophyly. Only one of the 11 described New World species of *Chaenusa s.l.* fits in *Chorebidella* (i.e., *Chaenusa bergi* (Riegel)). We acquired two Old World species in addition to *Cha. bergi* but only had permission to use one for DNA sequencing. As for *Chaenusa s.s.* extensive collecting will be needed to increase the representation of New World *Chorebidella* in future phylogenetic analyses.

Riegel (1950, 1982) defined *Chorebidella* using the following features: (1) 1st subdiscal cell open, (2) forewing vein RS+M absent, (3) stigma "short, wide", (4) labial palpi three-segmented, and (5) gonoforceps "not stocking-shaped in lateral view". Both species of *Chorebidella* included in this study have the 1st subdiscal cell open through the partial or complete absence of forewing veins 2-1A and 2cu-a, forewing vein RS+M absent, a relatively broad stigma, and gonoforceps that gradually narrow proximally to distally and are roughly triangular-shaped. *Chaenusa bergi* has three-segmented labial palpi, but *Chaenusa* sp. 3 has two-segmented labial palpi. Two-segmented labial palpi have not been recorded for any species of *Chaenusa s.l.*

CONCLUSIONS

The results of this study indicate that *Chaenusa s.l.* is not monophyletic, but *Chaenusa s.s.* and *Chorebidella* are monophyletic groups with moderate to strong support. *Chorebidea* was not monophyletic in any of the analyses, but four of five species of *Chorebidea* included in this study formed a clade in all analyses. The species of *Chorebidea* that did not form a clade with the other species of *Chorebidea* (i.e., *Chaenusa* n. sp. 3) exhibits morphological character states observed for species of *Chorebus*. Further, *Chaenusa* n. sp. 3 forms a clade with *Chorebus* in certain MP and

Bayesian analyses, and this suggests that *Chaenusa* n. sp. 3 may actually be a species of *Chorebus* with long curved setae on the eyes.

Phylogenetic analyses using ND1 gene sequences largely support Riegel's (1950, 1982) treatment of *Chaenusa s.l.* as *Chaenusa s.s.*, *Chorebidea*, and *Chorebidella*. However, we suggest that *Chaenusa s.l.* be retained until phylogenetic analyses with nuclear markers, morphology, and greater taxon sampling have been undertaken to confirm the relationships inferred in this study.

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NOTE

Observations on Flower Association and Mating Behaviour of the Pollen Wasp Species *Celonites abbreviatus* (Villers, 1789) in Greece (Hymenoptera: Vespidae, Masarinae)

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Celonites abbreviatus (Villers) ranges from Morocco across the entire North Mediterranean Area to Turkey. In the North it reaches the southern parts of Central Europe (Gusenleitner 1997). Most information on the bionomics stem from the Central European range of the species (Schremmer 1959, Blüthgen 1961, Bellmann 1984, 1995, Müller 1996, Amiet and Mauss 2003) whereas bionomical records from other parts of its distribution are rare (cf. Lichtenstein 1869, Ferton 1901, Fahringer 1922). Moreover, until now the mating behaviour of the species has been completely unknown.

On a field trip to the Maleas Peninsula of the Peloponnese (Greece, Laconias) *C. abbreviatus* was observed between the 5th and 10th of June 2005 at four localities in the vicinity of Profitis Ilias near Neapoli (I. 36°26.687′ N 23°06.926′ E, 55 m a.s.l.; II. 36°26.719′ N 23° 08.482′ E, 77 m a.s.l.; III. 36°26.122′ N 23°08.303′ E, 10 m a.s.l.; IV. 36°26.252′ N 23°07.012′ E, 20 m a.s.l.). All sites were situated in old, open fallow areas characterised by large patches of *Satureja thymbra* L. (Lamiaceae) with neighbouring *Phrygana* vegetation (Fig. 1) (Ordo Cisto-Micromeretalia Oberdorfer 54; cf. Horvat et al 1974). The ground was hard, stony and only sparsely covered with vegetation. An open source of water was present only in one of the localities.

Females of *C. abbreviatus* were frequently observed to visit flowers of *Satureja thymbra*. During the flower visits the proboscis was protruded into the corolla tube, indicating nectar uptake (Fig. 4). Simultaneously, the facial part of the head was rubbed over the nototribic anthers of the flower, and pollen grains accumulated on the frons of the female (Fig. 4), where modified setae form a pollen-collecting apparatus (Schremmer 1959, Müller 1996). At regular intervals the females interrupted nectar and pollen uptake and transferred pollen from the head to the mouthparts by alternating grooming movements of the forelegs and ingested the pollen (Fig. 5). On two occasions females of *C. abbreviatus* collected pollen from *Thymus capitatus* (L.) Ho. and Li. (Lamiaceae) at localities where

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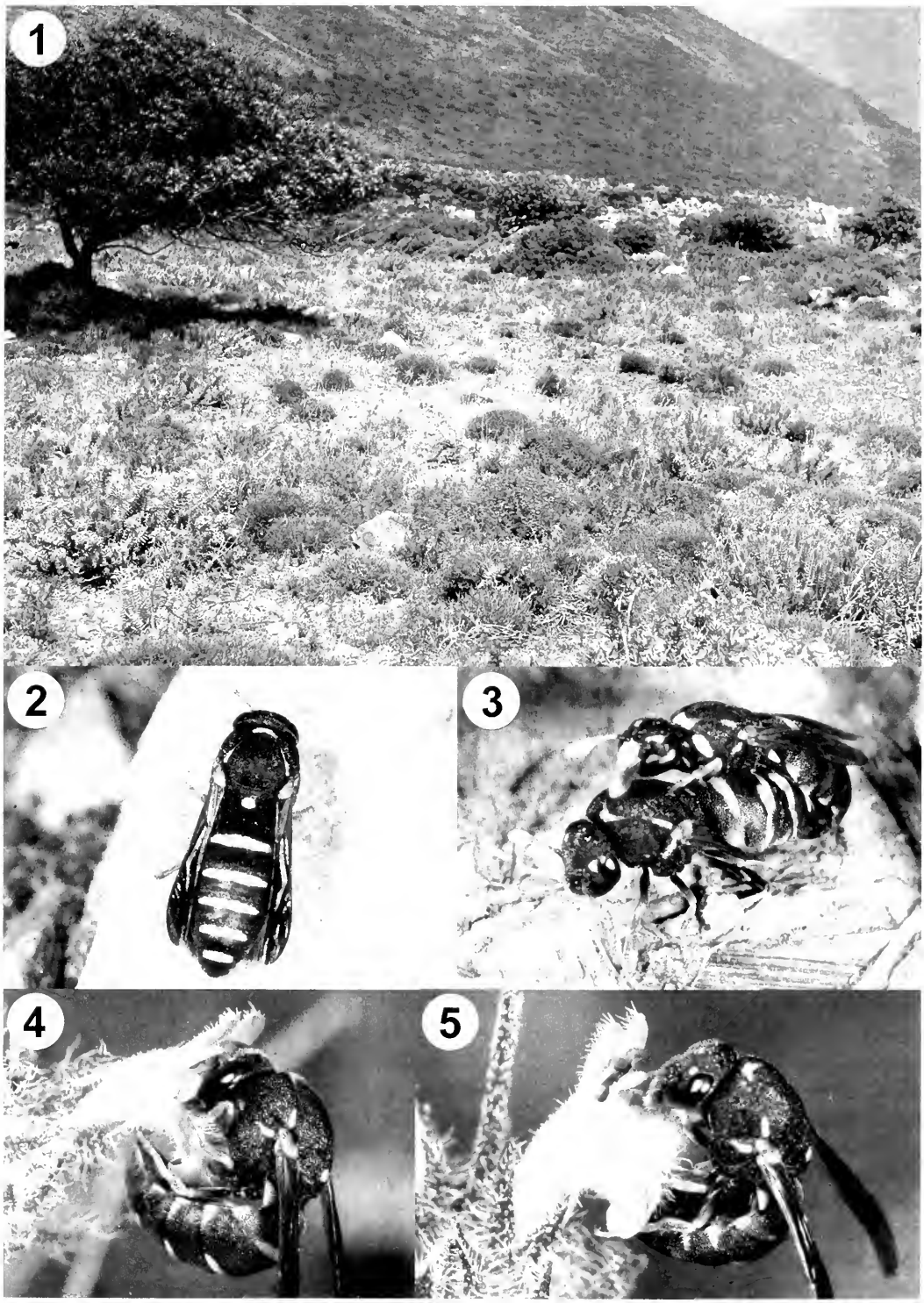
Figs 1–5. Habitat and behaviour of *Celonites abbreviatus* in vicinity of Profitis Ilias (Peloponnese, Greece). 1, Fallow area at locality II with large patches of *Satureja thymbra* (middle and right foreground), at which male and female pollen wasps were observed; *Phrygana* vegetation in background. 2, Female resting on sun-exposed stone. 3, Insertion phase of copulation; male clasping to the back of the female. 4, Female visiting flower of *S. thymbra*; her proboscis is protruded into the corolla tube, and the pollen collecting apparatus on the frons is



rubbed over the nototribic anthers. 5, Female transferring pollen from the fore-tarsal pollen comb of her left foreleg to her mouthparts, after grooming the pollen collecting hairs on the frons with the foreleg.

flowers of *S. thymbra* were nearly or completely withered. During visits to *T. capitatus* females stood with their middle and hindlegs on the lower lip of the flower, raised the anterior part of the body and rubbed the facial area of the head over the nototribic anthers, while the proboscis remained retracted. A single flower visit of a male was recorded at *S. thymbra*. The observed flower visiting behaviour of *C. abbreviatus* on the Maleas Peninsula adds further evidence that *C. abbreviatus* is specialised with regard to its pollen source to flowers of Lamiaceae since in Central Europe, Italy and Croatia pollen collecting of *C. abbreviatus* is also restricted to various flowers of Lamiaceae (e.g. *Acinos arvensis* (Lam.) Dandy, *Ballota nigra* L., *Ballota pseudodictamnus* Bentham, *Salvia officinalis* L., *Stachys cretica* L., *Teucrium montanum* L. and *Thymus* spec.; Bellmann 1984, 1995, Schremmer 1959, Müller 1996). Although imagines have been recorded also from flowers of other plants families such as Boraginaceae, Crassulaceae and Geraniaceae (Schremmer 1959, Schmiedeknecht 1930, Blüthgen 1961), these visits were probably for nectar uptake only (Schremmer 1959).

Between flower visits the females often alighted briefly on the ground or on small stones close to the forage plants (Fig. 2). On a single occasion a female defecated after alighting on a stone. Similarly, females of *C. abbreviatus* from Central Europe were frequently observed to alight on sun-exposed stones or on the ground in the vicinity of forage plants (Blüthgen 1961). A comparable behaviour is shown by females of the Afrotropical *Celonites clypeatus* Brauns (Gess 1993).

Males repeatedly patrolled flowers of *S. thymbra* flying at the level of the inflorescences. Copulations were observed in two instances. The first was initiated by a patrolling male that rapidly approached a female flying towards a plant of *S. thymbra*. The female responded, in that she flew about 0.2 m back from the plant, followed by the male which finally pounced on her. The pair fell to the ground, where a short period of grappling occurred of about one second, after which the male was positioned on the back of the female with his middle and hindlegs wrapped around the female's metasoma and his genitalia inserted into the genital chamber of the female (Fig. 3). The pair remained motionless in this position for about 10 seconds. Then the partners separated and flew away. The second copulation differed from the first in that the patrolling male pounced on a female visiting a flower of *S. thymbra*. During the following insertion phase the pair remained on the flower. The male released the female's body and fell over backwards but his genitalia remained in the female's genital chamber. After less than 10 seconds, the pair separated and both partners flew off. The female alighted on a nearby stone and cleaned her head with her forelegs, while the male flew off and disappeared. This is the first record of mating behaviour in *C. abbreviatus* and also the first description of the copulation of a species of the genus *Celonites*, in general. However, it has been recorded that males of Afrotropical species of *Celonites* also search for females in the vicinity of forage plants (Gess 1996: 59) indicating that resource based mating systems may be more widespread in this monophylum. The unusual position of the male in the second copulation looked similar to the hanging position in the first phase of the copulation of vespine wasps (cf. Schulz-Langner 1954). However, it remains to be shown whether this is a regular alternative mating position in *C. abbreviatus* or if the male accidentally lost his hold on the female's metasoma.

Imagines of *C. abbreviatus* were not observed at water, which is in agreement with the behaviour of *C. abbreviatus* in Central Europe (cf. Bellmann 1984, 1995) and of Afrotropical species of *Celonites* (Gess 1996: 107).

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The Genus *Allotilla* Schuster (Hymenoptera: Mutillidae): Phylogenetic Analysis of its Relationships, First Description of the Female and New Distribution Records

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Abstract.—The morphological characteristics of the monotypic genus *Allotilla* Schuster are discussed; new distribution records and a morphology-based phylogenetic analysis are presented, clarifying possible relationships with other sphaeropthalmine genera. Females of the genus are described and illustrated for the first time; male genitalia are illustrated.

Until now, *Allotilla gibbosa* Schuster, 1949 was known only from the holotype male from Cordoba, Argentina. In a list of Mutillidae from Argentina, Fritz (1998) included Buenos Aires as an additional collection locality for this species, without providing any additional information such as the number of specimens examined, their sex, or the depository. We must consider the Buenos Aires record not to be valid because it is incomplete and because we have been unable to locate any of Fritz's *Allotilla* specimens in his reference collections at the AMNH, New York (to which they were sold by his widow after his death) or at the Museo de Ciencias Naturales "B. Rivadavia," Buenos Aires (Roig-Alsina, pers. comm.).

The female of the Neotropical, monotypic genus *Allotilla* is described and illustrated for the first time; new distribution records and a morphology-based phylogenetic analysis are presented.

MATERIALS AND METHODS

We follow Brothers (1999) for the subfamily classification of the Mutillidae. For SEM examination we used a JEOL model JSM 5600. The *Allotilla gibbosa* specimens examined are deposited in the following institutions: American Museum of Natural History, New York (AMNH); Museum of Comparative Zoology, Harvard University , Cambridge (MCZ); Museo de Invertebrados G. B. Fairchild, Universidad de Panama (MIUP); D. J. Brothers's personal collection, University of KwaZulu-Natal, South Africa (DJBC); and Institut Royal des Sciencies Naturelles de Belgique (ISNB).

RESULTS

Allotilla Schuster

Allotilla Schuster 1949: 89–93. Type species: *Allotilla gibbosa* Schuster, 1949, by original designation and monotypy.

Generic characters of female.—Body covered with simple setae only. **Head**: almost round, narrower than mesosoma; eye small, nearly circular and flat (Fig. 3); genal carina absent; scrobal carina absent; antenna 12-segmented; antennal tubercle strongly projecting, with low lamellate ridge on anteromedial surface (Fig. 3); mandible slender, with preapical tooth nearly obsolete or totally absent (Fig. 3); mandible evenly arcuate on ventral margin, without tooth or constriction; proboscidal fossa with carina nearly reaching inner mandibular base; hypostoma without tooth or tubercle; maxillary palp 6-seg-

mented; labial palp 4-segmented, the second segment almost as long as wide. **Mesosoma**: broader than long, pyriform (Fig. 4); dorsum strongly convex, without transverse carina along posterior margin of pronotum or lateral carina; dorso-lateral margins without spines; scutellar scale absent; mesopleuron swollen; leg with apex of tarsus simple, not produced above claws. **Metasoma**: first metasomal tergum not constricted posteriorly, sessile with tergum 2 (Fig. 5); tergum II evenly convex, without rows of longitudinal carinae; tergum II with felt lines; sternum II without felt lines; tergum VI with surface totally sculptured and evenly merging with rest of tergum, pygidial area poorly defined by postero-lateral carina, only visible under high magnification (>30×) (Fig. 6).

Allotilla gibbosa Schuster, 1949
(Figs 3–8)

Allotilla gibbosa Schuster, 1949: 93–95, Holotype male, Argentina: Cordoba, col. W. M. Davis, Harvard University, MCZ, type 30516, examined.

Description of female.—Integumental color: head, mesosoma, all metasomal sterna, terga I, III and IV, reddish brown; antennae and legs yellow-red; mandible reddish brown except apical third blackish; tergum II reddish brown except posteriorly with two lateral, transverse, black spots interrupted medially; terga V and VI black. **Head**: vertex and gena with sparse, medium-sized punctures one or more diameters apart (Fig. 3); punctures of frons denser, less than one diameter apart; vertex and frons with long, sparse, erect and semi-erect, dark setae; gena, clypeus laterally and hypostoma with long, sparse, pale setae. **Mesosoma**: pronotum and mesonotum with punctures as on vertex (Fig. 4); metanotum with transverse reticulate band (Fig. 4); dorsum of propodeum mostly densely micropunctate-rugose (Fig. 4) except a narrow impunctate area near metanotum; mesopleuron with dense, medium-sized punctures, except for mostly impunctate anterior area near lateral area of pronotum; metapleura and lateral area of propodeum impunctate, smooth; setation of pronotum, mesonotum and metanotum similar to that of vertex; mesopleura and dorsum of propodeum with pale setae; metapleura and lateral area of propodeum glabrous. **Metasoma**: terga I and II with small, dense punctures, sparser in apical areas (Fig. 5); terga III and IV with small, sparse punctures; tergum V mostly smooth, except basal lateral area with a few punctures; tergum VI with scale-like surface sculpture basally, scales diminishing in size toward apex, gradually turning into granules (Fig. 6); sterna I and VI smooth; sterna II and III with small, somewhat sparse punctures; sterna IV and V mostly smooth, except apex with small, dense punctures; tergum I mostly with pale setae, a few dark setae at apex; tergum II with dark setae, except lateral area and apex with pale setae; terga III and IV mostly with pale setae; tergum V mostly glabrous, with a few pale and dark setae laterally; tergum VI glabrous; sterna I to V with pale setae; sternum VI glabrous.

Additional male characters.—The external male genitalia and the penis valve (Figs 7–8) are illustrated here for the first time (paramere, cuspis and digitus were described previously but not illustrated). The volsella has distinctive long setae on the cuspis apex (Fig. 7). The penis valve has a subapical tooth, more distant from the apical tooth than in males of *Protophotopsis* (see Figs 11–14, Cambra and Quintero 1997).

Material examined (56 males, 5 females).—All males were captured with Malaise traps (B. Garcete coll.) and females with pitfall traps (T. Delsinne coll.). PARAGUAY: **Boquerón** Department: Parque Nacional Teniente Enciso, Administración, 239 m (21 12′ S, 61 39′ W) 16–19 Sep 2003, 20 males [MIUP, DJBC]; same loc., 20–24 Mar 2004, 6 males [MIUP]; same loc., 23–26 Sep 2004, 3 males [MIUP]; Siracua, 275 m (21 02′ S, 61 45′ W) 20–22 Sep 2003, 21 males [MIUP, MCZ, AMNH, ISNB, DJBC]; Estancia Maria

Vicenta, 235–244 m (20°55′ S, 61°23′ W) 26–30 Sep 2004, 5 males [MIUP]; TransChaco, Mister Long, (20°35′ S, 62°02′ W), 17 Sep 2003, 1 female [MIUP]; Parque Nacional Teniente Enciso, TransChaco, 23–25 Sep 2004, 3 females [MIUP, ISBN, DJBC]; same data but 24–25 Sep 2003, 1 female [MCZ]. **Presidente Hayes** Department: Reserva Tinfunke, La Verde, 146 m (23°56′ S, 69°29′ W) 29 Nov–1 Dec 2003, 1 male [MIUP].

Variations.—Female frons dark reddish brown to black; tergum IV varying from totally reddish brown to black or the lateral areas black with reddish brown in the middle. Males from Paraguay are identical to the holotype, except that the propodeal lateral area is rugose on the holotype, but punctate with smooth areas to rugose-punctate or totally rugose in specimens from Paraguay. We consider this variation to be size-related: male rugosity increases with body length. In addition, larger males have the notauli nearly obsolete (same as the holotype), but notauli are absent in smaller males. Total length, females: 3.5–5 mm; males: 4–7 mm.

Distribution.—Paraguay and Argentina. *Allotilla gibbosa* was previously known only from the holotype from Cordoba, Argentina.

PHYLOGENETIC ANALYSIS

Taxa.—To test the subtribal position of *Allotilla* (currently included in the subtribe Pseudomethocina, Brothers 1975), and to recognize its phylogenetic affinities, we selected as the outgroup the following two genera: *Timulla* (Mutillini) and *Dasylabris* (Dasylabrini, genus not present in America); as ingroup taxa, we selected the following 17 Sphaeropthalmini genera, with mainly South American distributions and fully winged males: ten Pseudomethocina (*Euspinolia, Tallium, Atillum, Calomutilla, Horcomutilla, Pseudomethoca, Hoplocrates, Pappognatha, Hoplomutilla* and *Allotilla*), females with head transversely subquadrate, broader than the mesosoma, genal carina present (except *Euspinolia* and *Tallium*), first metasomal segment sessile, evenly merging with second; and seven Sphaeropthalmina (*Nanotopsis, Protophotopsis, Reedomutilla, Scaptodactyla, Limaytilla, Suareztilla and Limaytilla*), females with head nearly round, narrower than the mesosoma, and genal carina absent.

Characters.—Twenty-three binary and multistate characters of adult male (M) and female (F) external morphology and male genitalia were coded for analysis; all were treated as unweighted and unordered. No autapomorphies were used. The character matrix used is given in Table 1. The following characters were employed for cladistic analysis:

Head:

1. Head shape (F): 0—small, almost round, not broader than mesosoma; 1—transversely subquadrate, large, distinctly broader than mesosoma.
2. Head (M, F): 0—without large conical projection ventrally; 1—with large conical projection ventrally.
3. Scrobal carina (F): 0—present; 1—absent.
4. Genal carina (F):—absent; 1—present.
5. Mandible basal ventral margin (M, F): 0 - with constriction; 1—with broad lamellate projection; 2—almost straight.
6. Antennal tubercle (F): 0 - without lamellate projection; 1—with lamellate projection on anteromedial surface.
7. Antenna (F): 0–12-segmented; 1–13-segmented.
8. Ocelli (M): 0—small (diurnally active); 1—large (nocturnally active).

Mesosoma:

1. Dorsum of mesosoma (F): 0—longer than broad, sometimes as broad as or slightly broader than long; 1—distinctly broader than long.
2. Shape of mesosoma (F): 0—subrectangular; 1—violin- shaped, strongly constricted at the propodeal spiracles; 2—pyriform.
3. Axilla of mesonotum (M): 0—not expanded; 1—expanded posterolaterally as a rectangular or acute protruberance.
4. Scutellar scale (F): 0—present; 1—absent.
5. Notauli (M): 0—present; 1—absent.

Table 1. Data matrix for the 23 characters used in the phylogenetic analysis

Taxon	Characters																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
*Timulla**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
*Dasylabris**	0	0	1	0	0	0	0	0	0	2	1	0	1	2	0	0	1	2	0	0	0	0	0
Euspinolia	1	0	1	0	2	1	0	0	0	0	0	1	0	2	0	1	0	1	0	0	1	0	0
Tallium	1	0	1	0	-	-	0	0	0	0	0	0	0	2	0	1	0	1	0	0	1	-	0
Allotilla	0	0.	1	0	2	1	0	0	1	2	0	1	-	0	0	1	0	1	0	0	1	0	0
Nanotopsis	0	0	1	0	2	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0
Protophotopsis	0	0	1	0	2	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1	1	0	0
Scaptodactyla	0	0	1	0	2	1	0	1	1	2	0	1	0	0	0	1	0	2	0	0	0	1	0
Atillum	1	1	0	1	-	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0
Hoplocrates	1	1	0	1	1	0	1	0	0	1	0	1	0	1	1	1	1	1	0	0	0	0	0
Hoplomutilla	1	0	0	1	2	0	0	0	0	1	0	1	1	1	1	1	1	0	-	0	0	0	0
Pappognatha	1	0	0	1	1	0	0	0	0	2	0	1	1	1	1	1	1	1	1	1	0	0	0
*Pseudomethoca**	1	0	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
Calomutilla	1	0	0	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0
Horcomutilla	1	0	-	1	2	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
Xystromutilla	0	0	1	0	2	0	0	0	0	2	0	1	0	0	0	1	1	2	1	1	1	1	0
Reedomutilla	0	0	1	0	2	0	0	0	0	2	1	1	1	0	0	1	1	2	0	0	0	0	1
Suareztilla	0	0	0	0	2	0	0	0	0	2	1	1	1	2	0	1	1	2	0	0	0	0	1
Linaytilla	0	0	1	0	0	1	0	1	1	2	0	1	0	0	0	1	0	2	0	0	1	1	0

(- = not applicable or with intragroup variation)
*Only the type species examined: *Timulla dubitata* (Smith), *Pseudomethoca frigida* (Smith) and *Dasylabris* (*Dasylabris*) *maura* (Pallas).

6. Mesosternum posterior margin (F): 0—with short triangular or spiniform process; 1—with large truncate laminate process between and over inner margins of posterior coxae; 2—obsolete spiniform or triangular process.
7. Tarsomere 5 (M, F): 0—apex not produced above base of claws; 1—apex produced above base of claws, forming lamellate plate.
8. Pterostigma (M): 0—slightly sclerotized, membranous or absent; 1—heavily sclerotized.

Metasoma:

1. Tergum I (F): 0—broad, sessile with second apically; 1—nodose, disciform or petiolate, not sessile with second.
2. Tergum I (M): 0—broad, sessile with second apically; 1—subsessile-campanulate at apex; 2—nodose or petiolate with distinct lateral constrictions apically.
3. Tergum VI (F): 0—defined by lateral carinae; 1—not defined by lateral carinae.
4. Tergum VI (F): 0—mostly flattened, broad and generally totally sculptured (punctate, rugose, granulate or striate); 1—more convex, not broad, with a medial smooth area or entirely smooth.
5. Felt line on sternum II, lateral margin (M): 0—absent; 1—present.
6. Setae, 40× (M, F): 0—only simple; 1—both simple and plumose.
7. Parameres (M): 0—scarcely recurved apically or almost straight; 1—apex sharply and strongly recurved apically.

Characters of male genitalia not examined in all genera but considered potentially useful in a future phylogenetic analysis of the Sphaeropthalminae are: shape of cuspis, digitus and penis valve. The following characters were examined but not used because these characters need a more detailed study to determine if intragroup variation modifies them: length of antenna; eye size; sculpture of head; number of teeth on apex of mandibles; propodeum teeth; length of pterostigma and second submarginal cell.

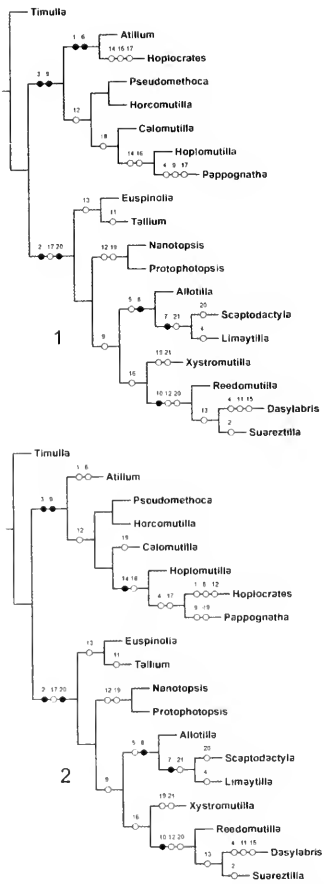
The following characters were examined but not used because they probably repre-

sent autapomorphies in the present analysis: posterolateral tubercles on vertex, present in some females of *Dasymutilla*, *Traumatomutilla* and *Cephalomutilla*; mandibles covered with dense, short pubescence, an autapomorphy of *Pappognatha*; humeral angle of pronotum produced as a hook-like tooth, an autapomorphy of *Gurisita* females (males unknown); posterior coxa with tooth apically on inner margin, an autapomorphy of *Vianatilla* females; tibia 2 with one apical spur, an autapomorphy of *Acanthophotopsis* males; males apterous or brachypterous, *Morsyma* (apterous), *Myrmilloides* and *Stethophotopsis* (brachypterous), *Dasymutilla* (rarely brachypterous); tergum II with arcuate transverse band of dense, curled setae and slight integumental ridge at anterior margin of band, in most *Dimorphomutilla* females; female with felt line on sternum II, autapomorphy of *Patquiatilla*; sternum II with anteromedian seta-filled pit, in some males of *Dasymutilla* and *Traumatomutilla*; tegula elongated to or beyond the level of transscutal articulation, autapomorphy for *Timulla* males; eye inner margin deeply and abruptly notched, autapomorphy for *Timulla* males.

A heuristic search of trees derived from parsimony analysis was carried out using NONA version 2.0 using WinClada version 1.00.08 (Nixon 2002), resulting in four cladograms. We preferred two of these minimal-length cladograms (Figs 1–2), see Results and Discussion. The following options were used: maximum trees to keep = 1000; number of replications (mult*N) = 1000; starting trees per rep (hold/) = 100; random seed = 1000; unconstrained search; search strategy of multiple TBR + TBR (mult* max*).

RESULTS AND DISCUSSION

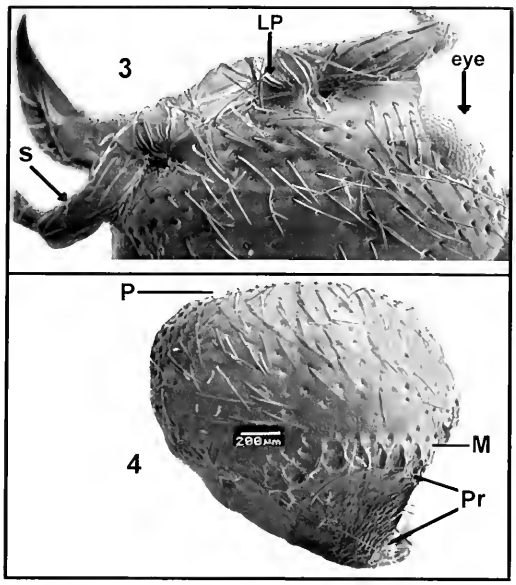
The female of *Allotilla gibbosa* was recognized based on morphological similarities to the known male, mainly the distinctive and peculiar inflation and broadening of



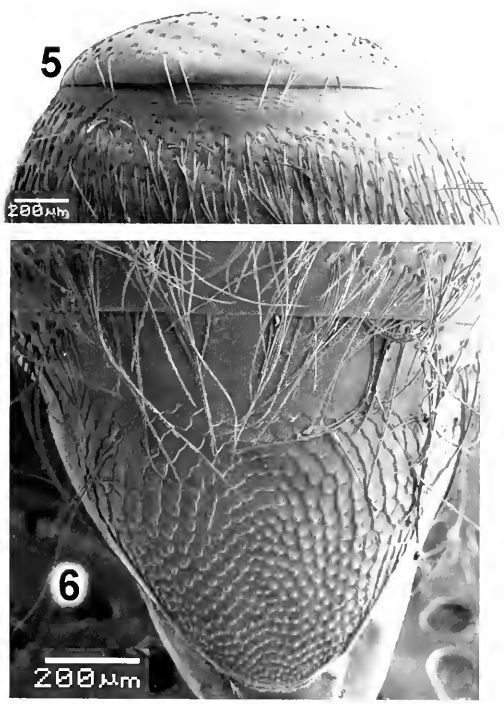
Figs 1–2. Preferred minimum-length cladograms of four trees derived from heuristic analysis of the character data presented in Table 1 using ratchet (WINCLADA) and mult* (NONA). Tree length = 62; consistency index = 0.43; retention index = 0.66. Synapomorphies are show by the black circles.

the mesosoma, and because these were the only female and male Sphaeropthalminae collected from the same geographic area, Paraguay's Chaco, that we recognized as belonging to a genus whose female was not known.

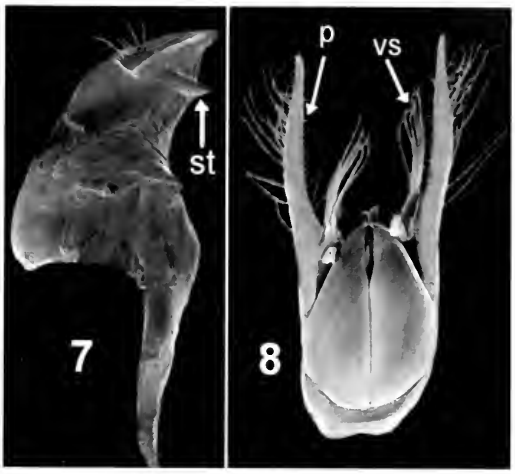
The relationships between American mutillid genera (none is known to be present outside of America, except for *Timulla*) and those of Africa and Australia are almost totally unknown, although different but closely related genera are involved. Vicariant biogeographical hypotheses and their common ancestral geo-



Figs 3–4. *Allotilla gibbosa*, female. 3. Head, dorsal view. 4. Mesosoma, postero-dorsal view. Abreviations: LP = lamellate projection of antennal tubercle, M = metanotum, P = pronotum, Pr = propodeum, S = scape.



Figs 5–6. *Allotilla gibbosa*, female metasoma, dorsal view. 5. Tergum 1 and basal part of tergum 2. 6. Tergum 6.



Figs 7–8. *Allotilla gibbosa*, male genitalia. 7. Parameres dorsal view. 8. Penis valve, lateral view. Abbreviations: P = paramere; ST = subapical tooth; VS = volsellar setae.

graphic areas suggest close evolutionary relationships with South American genera. Some genera widely distributed in the Americas, such as *Sphaeropthalma* and *Traumatomutilla*, cannot be included in the present cladistic analysis because they are as yet poorly defined.

The heuristic analysis resulted in four cladograms, the two preferred minimal-length cladograms (Figs 1–2) postulate a sister relationship of *Allotilla* with *Scaptodactyla* and *Limaytilla*. The other two cladograms postulate a less parsimonious, complex relationship for the selected South Amerian taxa and, following Occam's razor, were not accepted: *Allotilla* + [(*Scaptodactyla* + *Limaytilla*) + (((*Xystromutilla* + ((*Reedomutilla* + (*Dasylabris* + *Suareztilla*)))].

These preliminary cladograms suggest than *Allotilla* is more closely related to genera in the subtribe Sphaeropthalmina than to those in the Pseudomethocina. At present, we do not know of any unique morphological characters to separate these two subtribes.

The biology of *Allotilla gibbosa* is unknown, but the black integument, moderately sized eyes, and very small ocelli of the males suggest that they are diurnal. The following morphological characters of

Allotilla females indicate that they spend most of their lives underground: small, flattened eyes, relatively short legs with a fore tarsal rake (used to excavate soil), and a mostly reddish-brown integument. Extensive visual samplings carried out during daylight hours in Teniente Enciso National Park did not yield any *Allotilla* females from the ground or on the sparse vegetation; females were collected only with pitfall traps. These capture data lend support to the postulated underground, burrowing habits of the females. Probably they parasitize small, underground-nesting aculeates. Females of the here-recognized closely related sphaeropthalmine genera, *Scaptodactyla* and *Limaytilla*, sister genera to *Allotilla*, have a similar morphological habitus, suggesting that they have similar hypogeal lives and burrowing activities.

A morphology-based phylogenetic analysis of 18 mostly South American mutillid genera and one from outside America (*Dasylabris*) permits us to construct a hypothetical scenario of biogeographic divergences. The vicariant event that divided the population of the common ancestor of the taxa presented in Table 1 was the uplifting of the Andean high mountain range. This uplifting event was followed by ecological divergence of the two Andean regions: the elongated West costal region, draining into the Pacific Ocean, isolated from a more extensive and ecologically diverse Eastern region. The ancestor population of the present-day *Euspinolia*, an almost exclusively Chilean and Peruvian taxon, was isolated on the Pacific Andes slopes. The common ancestor of both *Tallium* and *Limaytilla* + *Scaptodactyla* + *Allotilla* was relegated to the region east of the Andes. The climatic and vegetational changes brought about by the Andean uplift, particularly the desertification of the Chaco region, was the driving selective force that caused the diversification and evolutionary split between *Tallium* and the sister genera of *Allotilla* + *Scaptodactyla* + *Limaytilla*.

Spichiger et al. (2004), investigating the geographical zonation in South America of 32 common tree species encountered in Paraguay, found that the xeromorphic forests of the Chaco area act as an edaphic barrier to many species that are centered in northern Argentina. The genus *Allotilla* is reported only from northern Argentina and Paraguay.

If additional sphaeropthalmine genera eventually are included in the data matrix presented here, the larger data matrix might provide a better resolution in the phylogenetic analysis.

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Parasitism and Sex Ratio of the Bedeguar Gall Wasp *Diplolepis rosae* (L.) (Hymenoptera: Cynipidae) in Sicily (Italy)

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Abstract.—The *Diplolepis rosae* gall community is analysed in Sicily (Italy), based on collections totalling 82 galls from 12 sites from which 1,026 adult insects were obtained. The gall wasp exits in March-June from galls induced the previous year. On average 5.6 *D. rosae* individuals per gall were obtained, corresponding to 44.8% of all the emerged insects. We obtained 4.3% of *D. rosae* males overall, the highest figure found till now for the cynipid overall in Europe, where male *D. rosae* are usually rarer, and the first record of them for the Mediterranean area. No inquilines were found, and, consequently, none of their specific parasitoids. However, *Eurytoma rosae*, generally considered as a specific parasitoid of the inquiline *Periclistus brandtii*, was obtained, together with the polyphagous *Exeristes roborator*. In all, seven parasitoid species emerged from the galls: four of them, *Orthopelma mediator*, *Torymus bedeguaris*, *Exeristes roborator*, and *Eupelmus urozonus*, start to emerge together with *D. rosae*, while *Glyphomerus stigma*, *Pteromalus bedeguaris*, and *E. rosae*, have their maximum peaks later in the year. All the cited species, except for *E. roborator*, showed a second peak of emergence in September, when *D. rosae* is absent. Parasitization ranged from 12.5 to 100%, reaching more than 70% in 66.6% of the samples, but it was rather low (30.5%) when males were present, even though there was no overall correlation between parasitization and *D. rosae* sex ratio. Statistical analysis showed however that all the parasitoid species (except for males of *T. bedeguaris* and *P. bedeguaris*) are longer (which we take to signify larger) than *D. rosae* males, and neither the size nor the sex ratio of parasitoids differed statistically depending on the presence of male *D. rosae*.

Diplolepis rosae (Linnaeus, 1758) is a palaearctic species, introduced in the nearctic region (Shorthouse and Ritchie 1984). It is widespread in peninsular Italy (Pagliano 1995), from where it has been known since at least 1600 (Tuscany: Pagliano et al. 1997), and in Sicily (De Stefani Perez 1887, as *Rhodites rosae* L.). Its multilocular galls have been recorded on 18 species of *Rosa* in Italy (De Stefani Perez 1887, 1902, 1905, Pellizzari Scaltriti 1988, Pagliano et al. 1997), and on 32 species in Europe and the Mediterranean basin (Houard 1908, Nieves-Aldrey 2001), though the gall wasp seems to prefer those species that are taxonomically allied in the Section Caninae (Randolph 2005), and particularly *R. canina* L. (Schröder 1967). Although *D. rosae* reproduces itself by amphitokous parthenogenesis (Beauvisage 1883, Callan 1940), males are reproductively inactive (Stille and Dävring 1980) and of spasmodic occurrence probably due to female infection with *Wolbachia* bacteria, which is also common in other *Diplolepis* species (Plantard et al. 1998, 1999). Larvae grow inside the galls and overwinter in diapause as prepupae; they pupate the following spring and emerge soon after (Schröder 1967). *Diplolepis rosae* galls host a large insect community that has been extensively studied in many countries (Randolph 2005, and references therein). Considering only Hymenoptera parasitoids, Noyes (2003) lists 29 species of Chalcidoidea, and numbers increase when parasitoids belonging to other superfamilies are included (Fulmek 1968). However, several of the names listed by Fulmek (1968) are invalid or misidentifications or probably erroneously associated with *D.*

Table 1. Differences in the number of males and in the percentage of parasitization in different groups of gall samples.

	Total number of *Diplolepis rosae* emerging	Average number of *D. rosae* emerging per gall	Sex ratio (No. males/No. females)	% of *D. rosae* males as total of emerged insects	Average parasitization
Sicilian galls collected from 1992 to 2005 (n = 76)	394	5.18 (min.: 0; max.: 92)	0	0	57.6% (min.: 12.5%; max.: 100%)
Sicilian galls collected in 1965 (n = 6)	66	11	0.43	21	30.5%
Hungarian galls collected in 2001 (n = 2)	42	21	0.31	15.6	34.3%

rosae (Askew pers. comm.). Despite this deep knowledge of biology and ecology of the bedeguar gall wasp all over Europe, little or nothing is known about it in Italy (cf. Randolph 2005). The aim of this study is to rectify that situation, with special emphasis on aspects needing further investigation (*D. rosae* sex-ratio and parasitism), as suggested by Randolph (2005).

MATERIALS AND METHODS

A total of 82 galls were collected in the following localities in Sicily (Italy) (in brackets the number of galls per sample): Madonie Mts. (Palermo), 13.IV.65 (6); Madonie, Piano Pomo 2.II.96 (1); Madonie, Piano Zucchi 18.II.96 (1); Madonie, Piano Cervi 30.V.96 (1), 31.V.01 (1); Madonie, Fosso Canna 6.VI.99 (1); Madonie, Castelbuono 13.X.96 (1); Madonie, loc. Vicaretto 27.X.96 (10); Ficuzza (Palermo) 16.III.97 (5), 7.IX.97 (9), 7.II.99 (3), 28.III.99 (1), 27.VI.99 (2), 19.III.00 (8), 6.II.05 (2); Contessa Entellina, loc. S. Maria del Bosco (Palermo) XI.92 (1); Bivona (Agrigento) 29.X.96 (16); Nebrodi Mts. (Messina), Biviere di Cesarò 2.XI.96 (1), 17.X.99 (2); Pergusa (Enna), 13.XI.04 (10). One additional sample was collected in Hungary (Fertö-Hanság National Park, Köszeg, 16.V.01, 2 galls). Galls of *D. rosae* examined during this study were collected on *Rosa canina* L., *Rosa sempervirens* L. and *Rosa* sp. Galls were placed separately in single small cages, at room temperature in the Palermo laboratory. They were kept for at least one year after the collecting date. In this way different emergence dates could be recorded for both gall inducers and parasitoids. Each emerged individual was counted, mounted and labelled. Parasitoid identification was carried out by M.C. Rizzo, if not differently reported in the Acknowledgements. Total body length, from the apex of the head to the tip of the abdomen, of all *D. rosae* adults and 30 specimens (males and females) of each parasitoid species was measured with the aid of a binocular microscope. Parasitoid length does not include the exserted ovipositor sheaths. Statistics were performed in STATISTICA (StatSoft 2003).

RESULTS AND DISCUSSION

Sex ratio and phenology of Diplolepis rosae.—A total of 460 individuals of *D. rosae* was obtained from the 82 galls examined, corresponding on average to 5.6 cynipids per gall and to 44.8% of all the emerged insects. However, while no males of *D. rosae* emerged from the 76 galls of 1992–2005, 21% males emerged from those collected in 1965 (Table 1). Also, in the latter sample, the average number of emerged *D. rosae* per gall was relatively higher (11 versus 5.18 of the other samples), while the percentage parasitization was somewhat lower than in the other samples on average (30.5 versus 57.6%) (Table 1). Table 1 also includes an occasional sample from Hungary, which also yielded a considerable number of males

Table 2. *Diplolepis rosae* sex ratio known until now (from Randolph 2005, except for the last five sets of data).

Country and Author	Total number of *D. rosae* individuals emerging	No. of males	% of males
USA: Kinsey (1920)	419	6	1.5
ENGLAND: Callan (1940)	6007	46	0.8
ENGLAND: Blair (1943)	104	2	1.96
ENGLAND: Niblett (1949)	601	1	0.17
NORTHERN ENGLAND: Askew (1960)	1264	51	4.2
DENMARK: Hoffmeyer (1925)	3425	137	4
GERMANY: Adler & Straton (1894)	671	7	1
GERMANY: Weidner (1956)	127	1	0.8
FRANCE: Hardouin (1943)	700	0	0
FRANCE, SPAIN, SWITZERLAND, AUSTRIA, SOUTH GERMANY: Schröder (1967)	2684	0	0
ENGLAND, ITALY, DENMARK, SWEDEN: Picard (1926)	>2000	4	<0.2
SOUTHERN SWEDEN: Nordlander (1973)	388	6	1.5
SPAIN: Nieves-Aldrey (1981)	249	0	0
SPAIN: Pujade Villar (1983)	49	0	0
SICILY (ITALY): this study (the whole Sicilian data set)	460	20	4.3
SICILY (ITALY): this study (Sicilian sample of 1965)	66	20	30.3
HUNGARY: this study (one sample, 2001)	42	10	23.8

(15.6% of the total insects); the number of cynipids emerged per gall (21) and percentage parasitization (34.3%) reflect those of the Sicilian sample of 1965 (cf. Table 1). Also considering Sicilian samples on the whole, *D. rosae* male percentage obtained during this study is among the highest reported in the literature (4.3%), and it is very much higher than the value given by Picard (1926) for Italy and other countries cumulatively (0.2%) (Table 2). High male figures for single samples, similar to those recorded by us (Sicilian sample of 1965: 30.3% of the total number of cynipids; Hungarian sample of 2001: 23.8%; cf. Table 2) are however reported by other authors (38%: Walsh 1924, 13%: Askew's unpublished data for a sample from Yorkshire (northern England), in Randolph 2005), even if never in the Mediterranean area. Askew (1960) suggested the presence of a decreasing latitudinal gradient (North>South) to explain the distribution of males of *D. rosae* in northern Europe, and data previously collected in southern Europe (reporting the complete absence of males) seemed to confirm his hypothesis (Nieves-Aldrey 1981, Pujade Villar 1983). Our results, however, lead us to reconsider the existence of a latitudinal gradient; alternatively, we suppose that emergence of *D. rosae* males could depend on the combined effects of environmental and biological factors (such as female infection with *Wolbachia* bacteria and its spatial and temporal diffusion), as other authors have already hypothesized (Shorthouse and Ritchie 1984, and references therein, Plantard et al. 1998, 1999).

The cynipid phenology recorded during this study in Sicily matches what is already known for the species in North and central Europe (Callan 1940, Schröder 1967, Stille and Dävring 1980, Randolph 2005), even if its cycle starts earlier, probably because of the warmer weather: the majority of *D. rosae* adults exited galls in March (Fig. 1), with a few individuals continuing to appear till the end of the spring as recorded also by Schröder (1967) in central Europe. Male *D. rosae* of the 1965 Sicilian sample were obtained in May and June, at the same time as females, in contrast to the finding of Callan (1940), who recorded male appearance distinctly earlier than that of females. During this study neither the

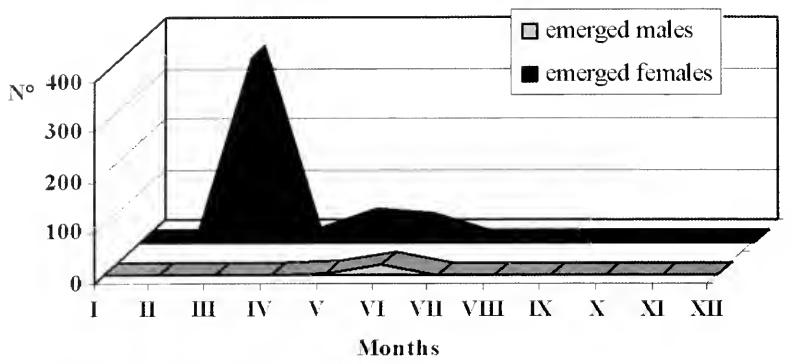

Fig. 1. Seasonal appearance of adults of *D. rosae* in Sicily.

inquiline *Periclistus brandtii* (Ratzeburg) nor its parasitoids were found. Altough sometimes a common inhabitant of *D. rosae* galls, this species has a variable distribution in central and northern Europe and seems rarer in Mediterranean countries (Nieves-Aldrey 1981, Pujade Villar 1983, Randolph 2005). In Italy it is known only from the north (Pagliano 1995). No other inquiline species has been reared during this study.

Parasitoid complex.—Although a large number of parasitic wasps is associated with the bedeguar gall wasp, a typical list of parasitoids comprises about a dozen species (Schröder 1967, Askew 1984, Randolph 2005). During this study a total of 566 Hymenoptera, mainly belonging to the most common *D. rosae* parasitoid species, was obtained from the Sicilian galls as follows: 374 *Orthopelma mediator* (Thunberg) (= *O. luteolator* Gravenhorst) (Ichneumonidae), 98 *Torymus bedeguaris* (Linnaeus) (Torymidae), 52 *Glyphomerus stigma* (Fabricius) (Torymidae), 23 *Pteromalus bedeguaris* (Thomson) (= *Habrocytus bedeguaris* Thomson) (Pteromalidae), 12 *Exeristes roborator* (Fabricius) (Ichneumonidae), 5 *Eurytoma rosae* Nees (Eurytomidae), and 2 *Eupelmus urozonus* Dalman (Eupelmidae). They represented 55.2% of all insects and their relative abundance is reported in Fig. 2.

Orthopelma mediator is an endophagous species, largely known as a widespread parasitoid of *D. rosae* (Askew 1960, Nieves-Aldrey 1981, Redfern and Askew 1992, Randolph 2005, and references therein), previously unrecorded from Sicily (Scaramozzino 1995, Noyes 2003). It was known as a parasitoid of *D. rosae* in Italy as early as 1600, since an unidentified Ichneumonidae, corresponding to it, is portrayed by Redi in an unpublished plate on *D. rosae* galls collected in Tuscany (Pagliano et al. 1997). In this study it was the most common (88.9% of the samples) and abundant parasitoid (66.1% of all parasitoids) (Fig. 2). *O. mediator* emerged from March onwards (Fig. 3), so that its phenology matches that of the gall inducer, as Nieves-Aldrey (1981) already observed in Spain, except in autumn when there was a late peak of emergences.

Torymus bedeguaris is a holarctic species (Grissell 1995, Noyes 2003), already recorded in Italy (De Stefani Perez 1905, Pagliano 1995, Pagliano and Navone 1995, Noyes 2003), mainly known as an ectoparasitoid of cynipid gall wasps belonging to the genus *Diplolepis* or of their inquilines (De Stefani Perez 1905, Askew 1960, Nieves-Aldrey 1981, Noyes 2003); it is also occasionally reported attacking *O. mediator* (Askew 1960, Schröder 1967). In Sicily *T. bedeguaris* represented 17.3% of all emerged parasitoids and its phenology overlaps that of *D. rosae* and *O. mediator* (cf. Figs 2 and 3). This trend is similar to that recorded by Nieves-Aldrey (1981) in Spain.

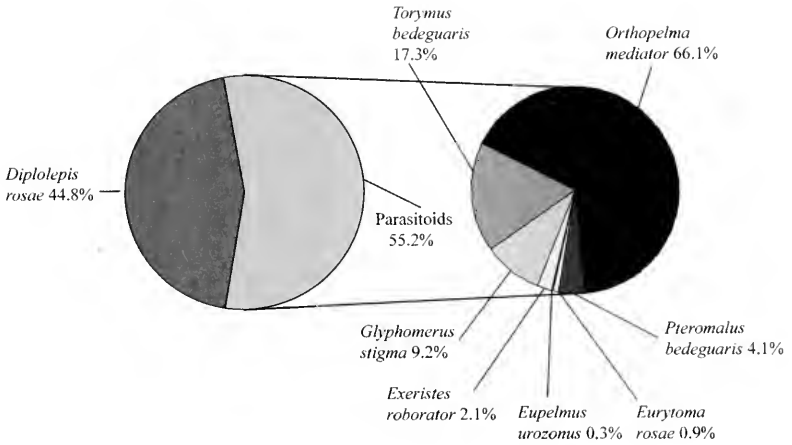

Fig. 2. Relative abundance of parasitoids of *D. rosae* in Sicily.

Glyphomerus stigma is another holarctic species typically associated with the genus *Diplolepis* (Noyes 2003), mainly known as an ectoparasitoid of *D. rosae* and its inquilines (Blair 1943, Askew 1960, Nieves-Aldrey 1981), and occasionally as a hyperparasitoid of *E. rosae* (Redfern and Askew 1992). This is the first record for Sicily, although the species was previously known from peninsular Italy (Pagliano 1995, Pagliano and Navone 1995, Noyes 2003). Nieves-Aldrey (1981) reported it as the second most abundant parasitoid in Spain; in Sicily it reached only 9.2% of all parasitoids (Fig. 2). It appeared later in the year than the inducers and the previous parasitoid species (Fig. 3), which agrees with the findings of Nieves-Aldrey (1981) in Spain.

Pteromalus bedeguaris is one of the two species of Pteromalidae typically associated with the galls of *D. rosae*. It is a holarctic species, hitherto unknown in Italy (Pagliano 1995, Pagliano and Navone 1995, Noyes 2003), although De Stefani Perez (1905) listed many other Pteromalidae as

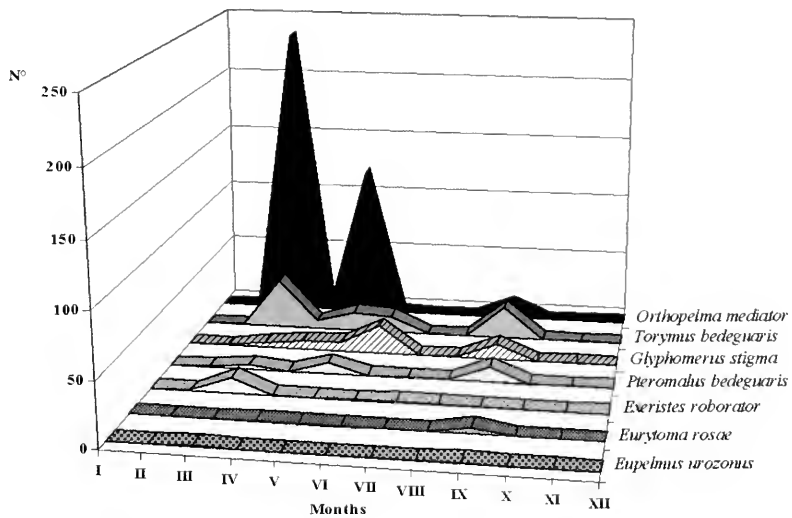

Fig. 3. Seasonal appearance of adults of parasitoids of *D. rosae* in Sicily.

parasitoids of *D. rosae* in Sicily. *Pteromalus bedeguaris* is considered a parasitoid of several species of *Diplolepis*, but it is also known to attack *O. mediator*, *T. bedeguaris* and *G. stigma* (Blair 1943, Redfern and Askew 1992, Noyes 2003), and occasionally parasitizes *Periclistus brandtii* (Nordlander 1973, Noyes 2003). The phenology of *P. bedeguaris* in Sicily shows two emergence periods, the first in late spring and the second in autumn (Fig. 3), similar to what Nordlander (1973) in Sweden and Nieves-Aldrey (1981) in Spain recorded. In the Sicilian samples, *P. bedeguaris* amounted to 4.1% of all emerged parasitoids (Fig. 2), while 22 individuals of this species (100% of all parasitoids) emerged from the Hungarian sample in June. This species is recorded as the second most common parasitoid in many countries of central Europe (Randolph 2005, and references therein). The palaearctic *Caenacis inflexa* (Ratzeburg) (Pteromalidae) was not obtained from any sample, being a specific parasitoid of the inquiline *P. brandtii* (Callan 1944), which itself was absent from our samples.

Exeristes roborator (Fabricius) is a palaearctic species, already known in Italy (Scaramozzino 1995). It is a polyphagous ectophagous parasitoid of Lepidoptera, Coleoptera and Hymenoptera larvae, known only as a parasitoid of *Biorhiza pallida* (Olivier) among Cynipidae (Fulmek 1968, Constantineanu and Pisica 1970). We cannot definitely affirm here that it is a primary parasitoid of *D. rosae*, even if no inquiline species emerged from our samples. Twelve individuals of this species (2.1% of all parasitoids) exited from the galls in March (Figs 2 and 3).

Eurytoma rosae is another palaearctic species, already known in Italy (Pagliano and Navone 1995, Noyes 2003), associated with galls induced by *Diplolepis* and considered as usually a specific parasitoid of *P. brandtii*, less commonly of *D. rosae* (Blair 1945, Claridge and Askew 1960). However, neither *P. brandtii* nor its specific parasitoid *C. inflexa* were found during this study, and the five individuals of *E. rosae*, which emerged in September (Figs 2 and 3), may have developed at the expense of *D. rosae*, in agreement with what Nieves-Aldrey (1981) recorded in Spain. The typical peak of emergences in late summer has been considered by many authors (Blair 1945, Niblett 1951, Claridge and Askew 1960) as a precocious emergence from galls of the same year.

Finally, *Eupelmus urozonus*, a cosmopolitan generalist (Pagliano 1995, Pagliano and Navone 1995, Noyes 2003) and occasional parasitoid of *D. rosae* (Schröder 1967, Noyes 2003) has been obtained during this study: two individuals of this bivoltine species (Askew 1961) emerged in March and September.

Parasitism and parasitoid relationships with the gall inducer.—Parasitization ranged from 12.5 to 100%, reaching more than 70% in 66.6% of the samples, in line with other authors who found the bedeguar gall wasp heavily parasitized (Schröder 1967, Nordlander 1973, Stille 1984). In Sicily, the *D. rosae* parasitoid complex comprises two groups of species; namely, a first group, including *O. mediator*, *T. bedeguaris*, and *E. roborator*, whose phenology overlaps and strictly follows that of the gall inducer, and a second group, with the prevailing species *G. stigma* and *P. bedeguaris*, which appears later in the year (Fig. 3). All the recorded parasitoid species, except for *E. roborator*, showed a late peak of emergences in autumn, when *D. rosae* is absent (Fig. 3). This peak has often been reported by other authors (see accounts above of single parasitoid species) and explained, depending on species, as a precocious emergence (i.e. for *E. rosae*) or as a bivoltine cycle (i.e. *E. urozonus*). Our present data do not allow us to decide which of the two explanations applies to *O. mediator*, *T. bedeguaris*, *G. stigma* and *P. bedeguaris*.

Moreover, it seems that there is a negative association between the presence of *D. rosae* males and parasitization (cf. Table 1),

Table 3. Summarized results for the one way ANOVA analysis (FD = 273; F = 49.67; $p < 0.001$) performed on the total length of male and female *D. rosae* and its parasitoids (small samples were excluded from analysis). *D. rosae* males are statistically shorter than all the parasitoid species, except for *T. bedeguaris* and *P. bedeguaris* males (in bold).

	D. rosae females	*D. rosae* males
O. mediator both sexes	longer*	longer
T. bedeguaris males	shorter	**not different**
T. bedeguaris females	longer*	longer
G. stigma females	not different	longer
P. bedeguaris males	shorter	**not different**
P. bedeguaris females	not different	longer

* Even if statistically longer, *O. mediator* and *T. bedeguaris* females overlap the maximum size of *D. rosae* females (Fig. 4), only *O. mediator* males being clearly longer. Moreover the two parasitoid species are much more slender than the massive *D. rosae* females, the latter probably being yet a suitable food source for them.

even if no correlation came out between parasitization and *D. rosae* sex ratio ($r = -0.3$; fd = 16, $p = 0.21$). Comparing total lengths of *D. rosae* adults (males and females) with total lengths of their commonest parasitoids through a one way ANOVA analysis, we found that *D. rosae* males are statistically much shorter than all the tested parasitoid species, except for *T. bedeguaris* and *P. bedeguaris* males (FD = 273; F = 49.67; $p < 0.001$) (Table 3 and Fig. 4). Given similar shapes of the species concerned, we take "shorter" to be a good indication of "smaller". From the ANOVA analysis parasitoid size did not differ between samples with or without males of *D. rosae* (cf. Fig. 4), and neither did their sex ratio differ (Wilcoxon Test; Z = 0.36; p = n.s.; fd = 4). However, our data are insufficient to ascertain whether *D. rosae* males represent an inadequate food resource for parasitoid development and/or whether galls which contain them are avoided by parasitoids. It would be interesting to compare parasitization percentages in other parts of Europe where good numbers of males of *D. rosae* are recorded.

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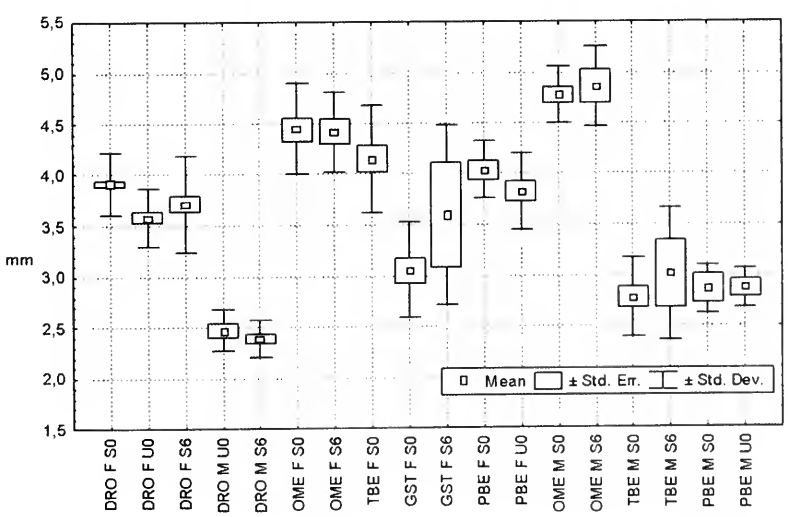

Fig. 4. Mean, s.d. and s.e. of the total length of male and female *D. rosae* and its parasitoids. (DRO = *D. rosae*; OME = *O. mediator*; TBE = *T. bedeguaris*; GST = *G. stigma*; PBE = *P. bedeguaris*; M = males; F = females; S0 = Sicilian samples 1992–2001; U0 = Hungarian sample 2001; S6 = Sicilian sample 1965).

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NOTE

Hylaeus punctatus (Brullé) (Colletidae), a Palaearctic Bee Long Established in South America

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The bee *Hylaeus punctatus* (Brullé) is recorded for the first time for Argentina, where it was introduced over thirty years ago, according to museum records. The introduction of *H. punctatus* into the New World has already been reported for the United States and Chile. Snelling (1983a) first recorded the species from southern California in 1981, and later Toro et al. (1989) reported its first sighting in the central region of Chile in 1986. The study of museum specimens reveals that *H. punctatus* was present in southern South America before these dates. Two specimens kept in the collection of the Museo Argentino de Ciencias Naturales in Buenos Aires were collected by the entomologist Adriana Oliva in the city of Buenos Aires in May 1976. Today the species is a common and abundant member of the bee fauna of the city of Buenos Aires and surrounding areas. This bee is further recorded here for two other, distant, localities in Argentina: the central west province of Mendoza and the Patagonian province of Río Negro.

This small colletid bee is native to the Mediterranean area of the Palaearctic Region (Dathe 1980, Snelling 1983a). It belongs to the subgenus *Spatulariella* Popov, all the species of which have a Palaearctic distribution (Michener 2000), with the only exception being *H. punctatus*, adventive in the New World. This species is easy to distinguish from the many native South American species of *Hylaeus* by the eighth metasomal sternum of the male. This sternum ends in a spoon-shaped expansion, which protrudes from the apex of the abdomen.

At least six exotic species of bees have become established in Argentina. Of these, only *Hylaeus punctatus* is deemed to have been introduced accidentally into this country. Other species have been purposely introduced, or have been introduced into neighboring countries and later dispersed to Argentina. Two species, *Apis mellifera* L. and *Megachile rotundata* (Fabricius), were introduced for economic purposes at various times. A fourth species, the Palaearctic *Bombus ruderatus* Fabricius, was introduced into Chile for pollination, and later expanded its range into southern Argentina (Roig Alsina and Aizen 1996). A fifth species, *Lithurgus huberi* Ducke, is widespread in Brazil, where it occurs from the northern state of Para to Minas Gerais and São Paulo (Silveira et al. 2002). It occurs in Argentina in the province of Misiones (San Ignacio, Museo Argentino de Ciencias Naturales, new record). According to Snelling (1983b) this species belongs to the Indo-Australian group of *Lithurgus atratus* (Smith); moreover, he found no morphological differences by which *L. atratus* may be separated from *L. huberi*, considering that this species is adventive in Brazil, probably introduced by man in historical times. Another exotic species present in Argentina is the Old World *Anthidium manicatum* (L.). This species has been recorded for the province

of Buenos Aires by Michener (2000). *Anthidium manicatum* also occurs in the eastern and southern states of Brazil, where it would have been introduced from Europe (Silveira et al. 2002); according to these authors the species, although broadly distributed in Brazil, seems to be rare. Finally, a likely candidate to become established in Argentina in the near future is *Bombus terrestris* (L.), which was introduced into Chile for pollination in 1997 (Estay and Vitta 2004). This bee is expected to follow the same route across the low southern Andes into western Patagonia as did *Bombus ruderatus* in the early 1990's.

Hylaeus punctatus has been collected in the Buenos Aires area in urban and suburban, as well as in natural habitats. In the city of Buenos Aires it is common in parks, and has been collected visiting flowers on balconies of buildings up to the seventh floor. Both males and females are common. The bee has been found in urban habitats in the provinces of Mendoza and Río Negro, in house gardens in the city of Mendoza, and in house gardens of the town El Bolsón in the latter province. Many records of flower visitation correspond to introduced exotic plants, such as *Eryobotria japonica* (Thunb.) Lindl., *Lavandula officinalis* Chaix, *Mentha aquatica* L., and *Alyssum sp.* Specimens have also been collected on *Asclepias curassavica* L., *Eryngium sp.*, and *Baccharis pingraea* DC., all of which are native plants. Toro et al. (1989) recorded that the bee flies late in the season in Chile, but collecting dates in the area of Buenos Aires indicate that the bee is active from spring (October) to late summer (May).

The following is a list of the collection records for *H. punctatus* in Argentina. Specimens studied and cited below are housed at the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" in Buenos Aires, Argentina.

Buenos Aires City: Palermo, V-22-1976, in house garden on flowers of *Eryobotria japonica* (A. Oliva); Villa Crespo, IV-14-1985, in balcony on 7th floor (A. Roig A.); Botanical Garden, Facultad de Agronomía, XII-29-1994 (A. Roig A.); Parque Centenario, X-31-1995, in balcony on 7th floor on flowers of *Alyssum sp.* (A. Roig A); Colegiales, I-18-1996, in house garden on flowers of *Asclepias curassavica* (A. Oliva); Colegiales, II-12-1996, in house garden on flowers of *Mentha sp.* (A. Oliva); Palermo, II-6-2003, in park on flowers of *Lavandula officinalis* (A. Roig A.). *Province of Buenos Aires:* Partido de Vicente López, La Lucila, II-17-1985 (L. Moffatt); Partido de Tigre, 12 km NW Tigre, I-20-1990, on flowers of *Eryngium sp.*(A. Roig A.); Partido de Escobar, Maquinista Savio, I-5-1997, on flowers of *Baccharis pingraea* (A. Roig A.); Partido de Vicente López, La Lucila, I-1-2003 (A. Roig A.); Partido de Hurlingham, Estación Experimental Inta Castelar, XI-6-2003, on flowers of *Lithrea molleoides* (Vell.) Engl. (L. Compagnucci & A. Roig A.). *Province of Mendoza:* Mendoza city, II-15-1994, in house garden on flowers of *Mentha aquatica* (A. Roig A.). *Province of Río Negro:* El Bolsón, II-3-1994, in house garden (A. Roig A.).

Species of *Hylaeus* nest in pre-existing holes and crevices, mainly in wood and twigs, but in other materials as well. This nesting behavior has surely facilitated the transport by man of these bees for long distances, carried along with their nesting substrates. The type of nesting behavior among bees is tightly correlated with their chance of becoming introduced species. There are two main types of nests (Malyshev 1935, Stephen et al. 1969, Michener 2000): those of burrowing bees, which have an excavated tunnel (usually in the soil) leading to the cells, and those of non-burrowing bees, which are constructed in the open or taking advantage of preformed cavities. Although there are certain species of bees with intermediate behaviors (Stephen et al. 1969), and there are certain lineages in which both types of behavior are present, this classification holds for entire lineages of bees. Most species of bees that have been introduced accidentally into exotic areas are non-burrowers. For example, of fourteen species reported that have accidentally become established in the United States (Daly 1966, Eickwort 1980, Snelling 1983a, Mangum and Brooks 1997), thirteen of them are non-burrowing bees.

These bees belong in the genera *Anthidium* Fabricius, *Chelostoma* Latreille, *Hoplitis* Klug, *Lithurgus* Berthold, and *Megachile* Latreille of the family Megachilidae, *Ceratina* Latreille of the family Apidae, and *Hylaeus* Fabricius of the family Colletidae. As another example, the only two exotic species that occur in Brazil (Silveira et al. 2002) which have been accidentally introduced, belong to the genera *Anthidium* and *Lithurgus*. All these groups nest in preexisting holes or crevices.

Available records and distribution suggest that *H. punctatus* is mainly associated today with human-modified habitats in Argentina. The dispersal of this species within the country (city of Mendoza, and El Bolsón town) may have been mediated by human transport, in a similar way in which the species first came to the country. There are no existing records in intermediate places between Buenos Aires and these two distant localities, although surveys have been conducted. In the province of Buenos Aires it has penetrated agricultural (Hurlingham, Escobar) and natural habitats (Tigre), where it has been recorded visiting native plants. On this ground, the progressive expansion of the bee to other areas in Argentina can be predicted.

The possible geographic origin of the invasive population in California was discussed by Snelling (1983a). He argues that this population matches more closely the color variant found in southern Europe, than the darker forms found in central Europe or the more extensively pale marked specimens of the subspecies *H. punctatus longinaculus* Alfken. In this respect the populations from Argentina agree with the pattern described by Snelling. Since introduction in Argentina antedates introduction in the U.S.A., the California population may have originated either from Europe or from Argentina. The same may be argued for the Chilean population. At least a dispersal from Argentina to Chile seems feasible, taking into account the invasion of other hymenopterans that have dispersed from Argentina to Chile, for example the paperwasp *Polistes buyssoni* Brèthes (Pérez D'Angello 1970). Of course, the dispersal of *Hylaeus punctatus* to the New World may have occurred independently several times from the Old World. The various possibilities of dispersal are difficult to assess without appropriate methods, such as a phylogeographic molecular analysis, beyond the scope of this contribution.

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Skeletal Anatomy of the Mesosoma of *Palaeomymar anomalum* (Blood & Kryger, 1922) (Hymenoptera: Mymarommatidae)

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Abstract.—Detailed study of the skeletal anatomy of the mesosoma of *Palaeomymar anomalum* was undertaken, primarily with SEM. Four previously unrecognized putative autapomorphies for the Mymarommatidae were discovered: 1) absence of a functional anterior thoracic spiracle; 2) fusion of the propleural arm with the profurcal arm; 3) presence of a pair of rods on the anterior surface of the prophragma; and 4) absence of the metafurca. The presence of a concealed prepectus fused with the posterolateral margin of the pronotum was confirmed. Additional features of possible significance for evaluating the phylogenetic position of Mymarommatidae are described and discussed. A sister-group relationship with the Chalcidoidea is the most well supported hypothesis presently, but needs additional corroboration.

The small family Mymarommatidae is arguably the most enigmatic wasp taxon. Eight extant and ten extinct species have been described (Grimaldi and Engel 2005). The biology of these minute wasps is almost entirely unknown. They appear to be associated with leaf litter and were reared once from a bracket fungus (Gibson et al. 1999). Because of the small size of the adults (immatures are unknown), it has been suggested that they are egg parasitoids, but this is entirely conjectural. The absence of biological information for Mymarommatidae is all the more intriguing because they display a number of highly unusual autapomorphic features, which in the case of head anatomy border on the bizarre—the occipital region is separated from the remainder of the head capsule by an expanse of pleated membrane that allows the head to expand and contract in an accordion-like manner (see Gibson 1986, fig. 9). Also, the prosternum and propleura are extensively fused, forming a continuous carapace in external view; the mesopleuron is fused along most of its posterior margin to the metapleuron-propodeum (Gibson 1986, fig. 10); the fore wing has a reticulate pattern on the surface (not to be confused with true wing venation; Gibson 1986, fig. 30); and the hind wing is reduced to a rodlike structure that apically is bifurcate to clasp and support the base of the forewing (Gibson 1986, fig. 33). Further putative autapomorphies are discussed by Gibson (1986) and Gibson et al. (1999) (see also below).

While there has never been any serious doubt about the monophyly of the Mymarommatidae, their phylogenetic position within the Hymenoptera is less well corroborated. Debauche (1948) was the first to place them in their own family (Mymarommidae [sic]), removing them from Mymaridae. This was reversed by some subsequent authors. The first comprehensive discussion of mymarommatid affinities in a cladistic context was undertaken by Gibson (1986), who placed them as sister group to the Chalcidoidea. The main evidence for this is the presence of axillar phragmata, apodemes projecting

under the mesoscutum and accommodating the origins of the mesotergal-trochanteral muscles (Gibson 1986, 1999, Gibson et al. 1999). This hypothesis was later supported by the phylogenetic analyses of Ronquist et al. (1999).

Debauche (1948) provided an overview of the anatomy of *Palaeomymar anomalum*. Gibson (1986) and Heraty et al. (1994) treated selected aspects of mesosomal anatomy in considerable detail, but a comprehensive survey of this body region in Mymarommatidae is wanting. The present paper examines the external and internal skeletal anatomy of the mesosoma and anterior part of the metasoma (the petiole) for *P. anomalum*. Findings will be discussed in a phylogenetic context, drawing on information obtained from ongoing surveys of the mesosoma in Hymenoptera in general and Chalcidoidea in particular, undertaken by L. Vilhelmsen and L. Krogmann, respectively.

MATERIALS AND METHODS

Examined material.—*Palaeomymar anomalum* (Blood & Kryger, 1922). GERMANY, Niedersachsen, Lüchow-Dannenberg, NSG Forst Lucie. Car net. 15.viii.2001. Leg. H. Meybohm. 5 females. Specimens and vouchers deposited in Zoologisches Museum Hamburg. SWEDEN, Sm[åland], Älmhults kommun, Stenbrohult, Djäknabygds bokbacke, N56°36.548', E14°11.583' (=Trap ID 24). Heath with old beeches. 1.–18.viii.2003 (=coll. event ID 818). Leg. Swedish Malaise Trap Project (Swedish Museum of Natural History). 6 females. Specimens and vouchers deposited in the Zoological Museum, University of Copenhagen.

Procedure for slide mounting.—Two specimens were dissected and mounted on a slide in Entellan.

Procedure for SEM-investigations.—Specimens were cleaned in a sonicator and dissected with small razor blade scalpels and minutien needles. The preparations were macerated in KOH for a few hours at 40°C or overnight at room temperature, rinsed in demineralised water and transferred to 70% ethanol. They were then transferred through a series of intermediate concentrations to absolute ethanol, which served as the transition medium for critical point drying. After critical point drying, the preparations were mounted on stubs with double-adhesive tape and coated with platinum prior to examination in a Jeol JSM-6335F field emission SEM unit.

RESULTS

The mesosoma of *Palaeomymar anomalum* is a compact structure. It can be subdivided into four major components that are comparatively easily separated by dissection (Fig. 1): 1) the pronotum; 2) the propectus, comprising the propleura and prosternum and accommodating the head articulation and foreleg attachments; 3) the mesonotum and attached pro- and mesophragma; 4) the mesopectus-metathorax-propodeum complex. The latter is by far the largest part of the mesosoma and is extensively fused to a degree where the boundaries between the individual parts are not obvious.

In the following, each of these regions are described in turn. In addition, we describe in detail the anterior part of the petiole comprising the mesosoma-metasoma articulation.

Pronotum.—Pronotum narrow medially (Fig. 3), laterally expanded into trapezoidal flange (Figs 2, 3); posteriorly articulating with mesopectus, ventrally with propectus (Fig. 1); with sparse, striate sculpture, except for small median band of dense, raised longitudinal striations (Fig. 3); sublaterally with deep dorsal depression posterior to distinct vertical carina extending almost entire height of pronotum (Figs 2, 3). Anteromedian margin in frontal view distinctly incurved (Fig. 3), forming slightly upturned lip just anterior of transverse pronotal sulcus; internally, anteromedian margin inflected, the median part of pronotum with concavity accommodating prophragma (Fig. 5). Dorsal margin in

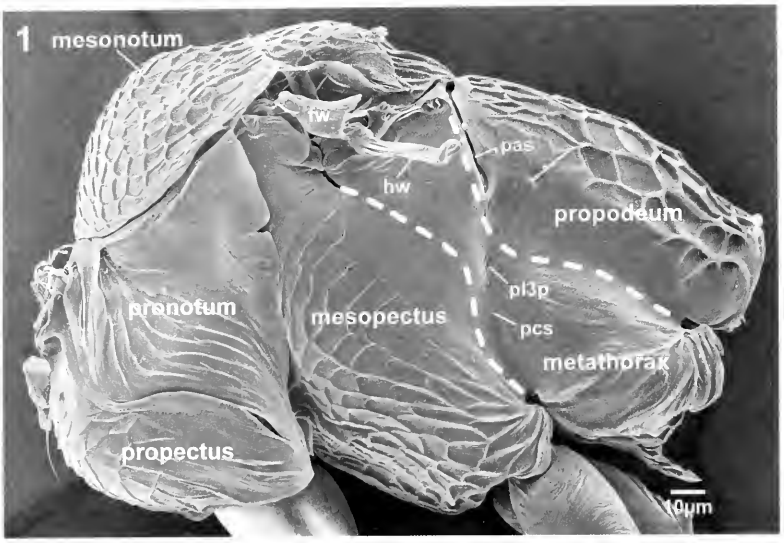
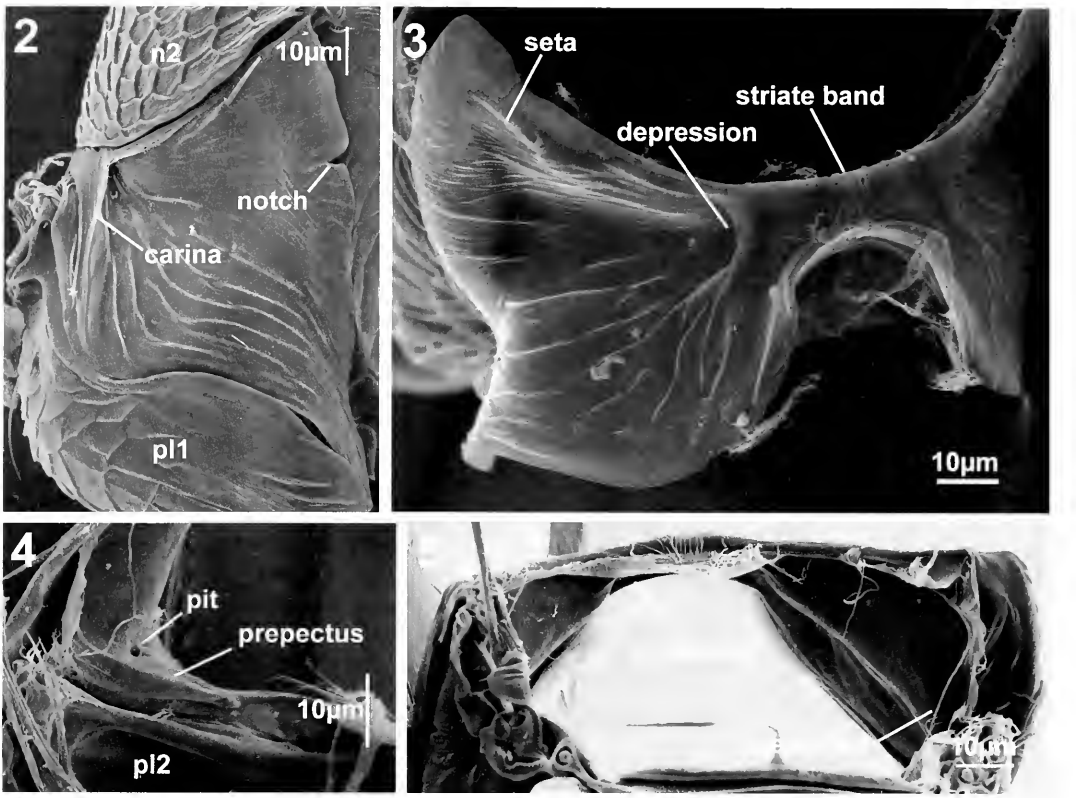


Fig. 1. Lateral view of mesosoma of *Palaeomymar anomalum*. Stippled lines indicate approximate boundaries between mesopectus, metathorax, and propodeum. Abbreviations: fw = fore wing base; hw = hind wing; pas = propodeal antecostal suture; pcs = paracoxal sulcus; pl3p = metapleural pit.

dorsal view deeply incurved, in lateral view with long seta laterally close to dorsal margin (Figs 2, 3). Posterolateral margin almost straight, with small notch about 1/3 of total height from posterodorsal corner (Fig. 2); posteroventral corner extended ventrally between pro- and mesopectus, slender (Fig. 2). Internally, pronotum predominantly smooth, posterolateral margin flanking low vertical carina (Figs 4, 5), the carina (interpreted as the prepectus, see discussion) extending for some distance, but neither reaching dorsal nor ventral margin of pronotum, and deflected anteriorly prior to reaching dorsal margin; small pit just anterior of carina (Fig. 4) associated with narrow strands of tissue. Anterior thoracic ('mesothoracic') spiracle not observed internally or externally.

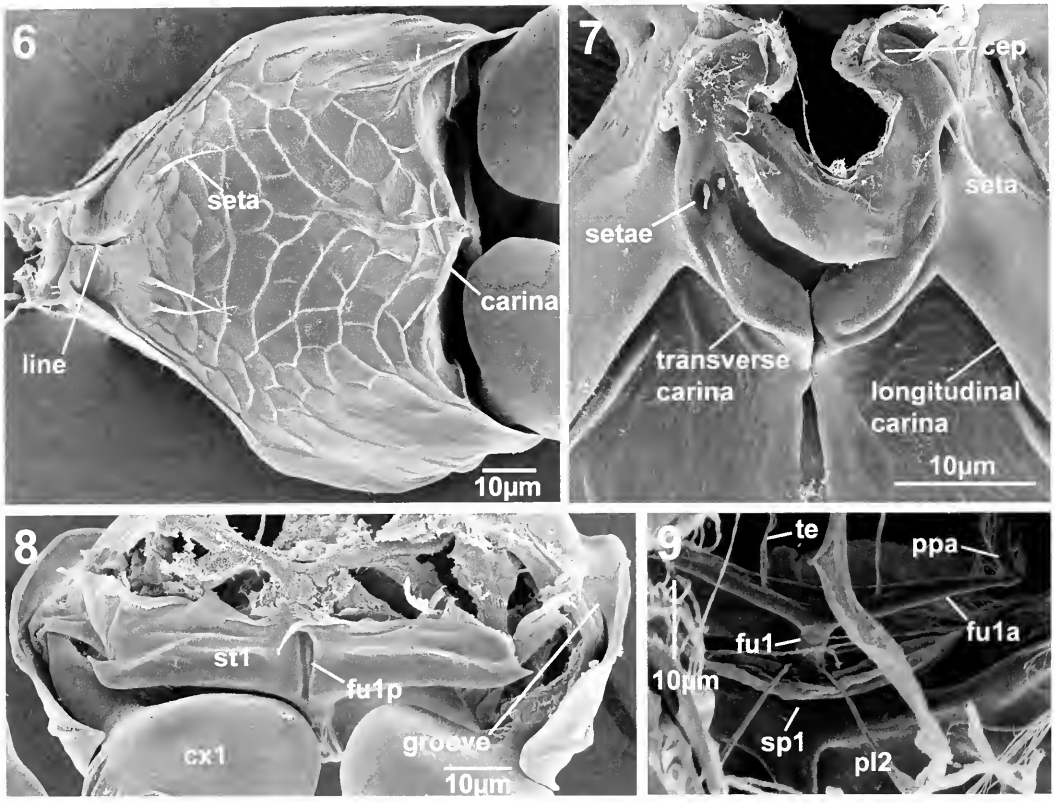
Propectus.—Propleural cervical prominence (Fig. 7, cep) with head articulation at anterodorsal corner of propectus, not retracted, separated from rest of propleura by transverse carina (Fig. 7); two short setae situated anteriorly of carina, one posteriorly. Cervical swellings with patch of sensilla, otherwise not developed. Propleura in ventral view linearly separated anteromedially, fused posteromedially (Figs 6, 7); anteriorly with 1 or 2 elongate setae sublaterally (Fig. 6); posteriorly with carinate margin slightly extended posteromedially (Fig. 6). Propleura laterally with an oblique longitudinal carina separating lateral, dorsal smooth part from ventrally reticulate surface; posterior part of carina laterally delimiting distinct groove accommodating lateroventral margin of pronotum and proximal part of procoxa (Fig. 8). Internally, propleural arm on posterodorsal corner of propleuron slender, projecting posteriorly, posterior end fused with lateral end of profurcal arm (Fig. 9, ppa). Prosternum (Fig. 8, st1) reduced in size, inflected at an angle of about 90 degrees relative to posterior part of propleura and not visible externally (Fig. 6); extensively fused with propleura ventrally, the boundary of fusion indiscernible; externally smooth, expanded dorsally of narrow procoxal cavities, separate from propleura laterally and with slit-like profurcal pit medially (Fig. 8, fu1p). Internally, profurcal base narrow, not extending far anteri-



Figs 2–5. Pronotum of *P. anomalum*. 2. Exterior lateral view. 3. Exterior anterior view. 4. Interior view of pronotal-mesopectal juncture showing prepectus (dorsal surface to left). 5. Interior, posterior view. Abbreviations: n2 = mesonotum; pl1 = propleuron; pl2 = mesopleuron.

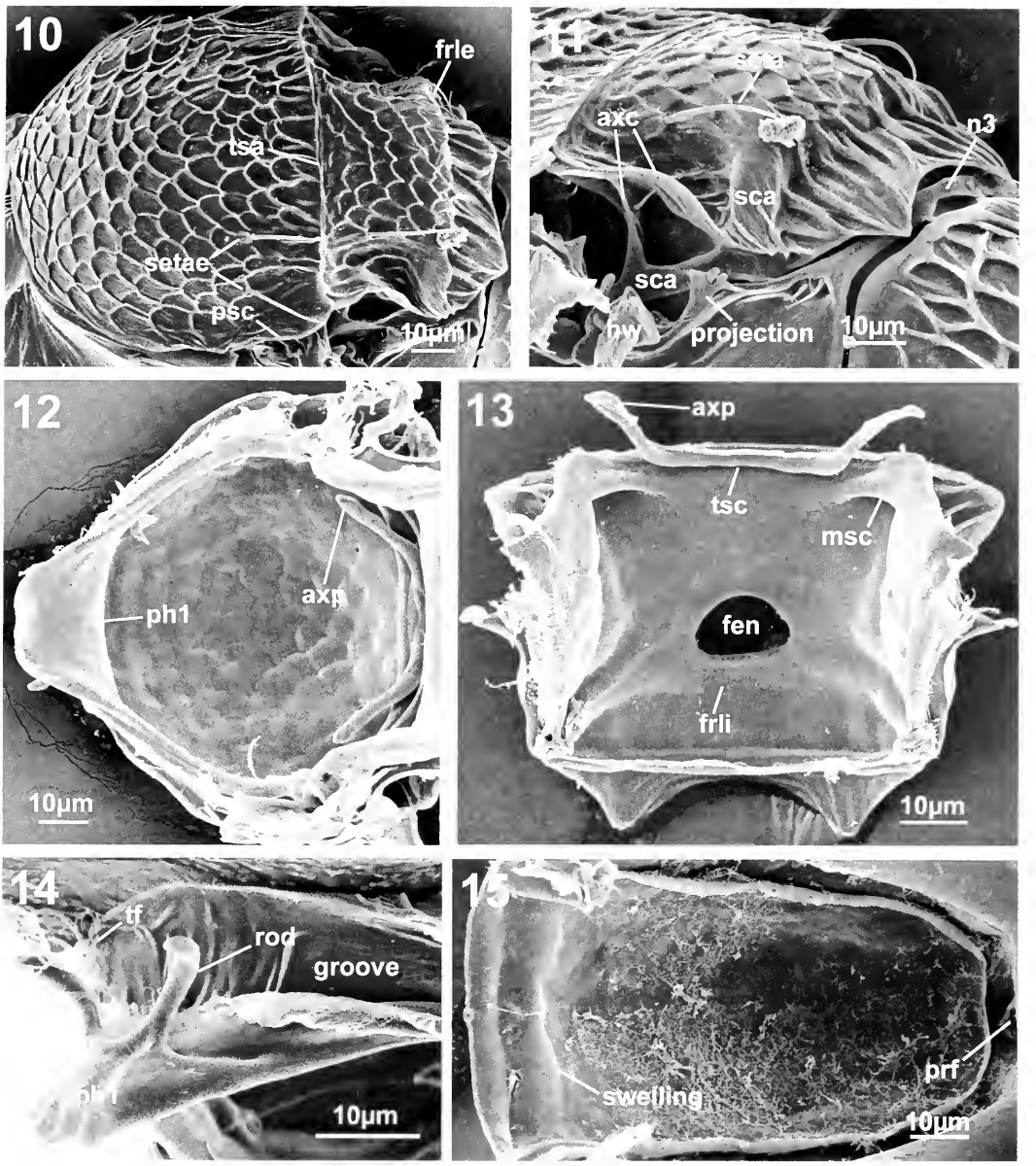
orly (Fig. 9, fu1), profurcal arms slender, extending laterally (Fig. 9, fu1a); profurcal bridge absent, anterior profurcal apodemes not developed, only slender tendons present sublaterally (Fig. 9, te). Procoxae very reduced proximally, without transverse carina. Katepisterna and prosternal sclerites not observed.

Mesonotum.—Externally, mesonotum predominantly with reticulate sculpture (Fig. 10). Internally, prophragma well developed, projecting anteriorly under pronotum, not subdivided medially nor extended laterally (Figs 12, 14, ph1); dorsal surface of prophragma with paired, anteriorly projecting, slender cylindrical rods submedially, the rods extending at an angle of approx. 90 degrees to each other (Fig. 14) but continuous medially, sometimes with tonofibrillae (Fig. 14, tf) distally and apparently closely associated with dorsomedian margin of pronotum. Mesoscutum with transverse groove just dorsal to rods between its external surface and prophragma accommodating dorsal margin of pronotum. Mesoscutum with median mesoscutal sulcus, notaulus, and parapsidal lines entirely absent externally and internally (Figs 10, 12); with two elongate setae posterolaterally just anterior to transscutal articulation (Fig. 10); transscutal articulation complete, straight (Fig. 10, tsa); parascutal carina well developed laterally, overhanging posterodorsal margin of pronotum and fore wing articulation point (Fig. 16, psc) and extending posterior to lateral end of transscutal articulation (Fig. 10, psc), with two elongate setae



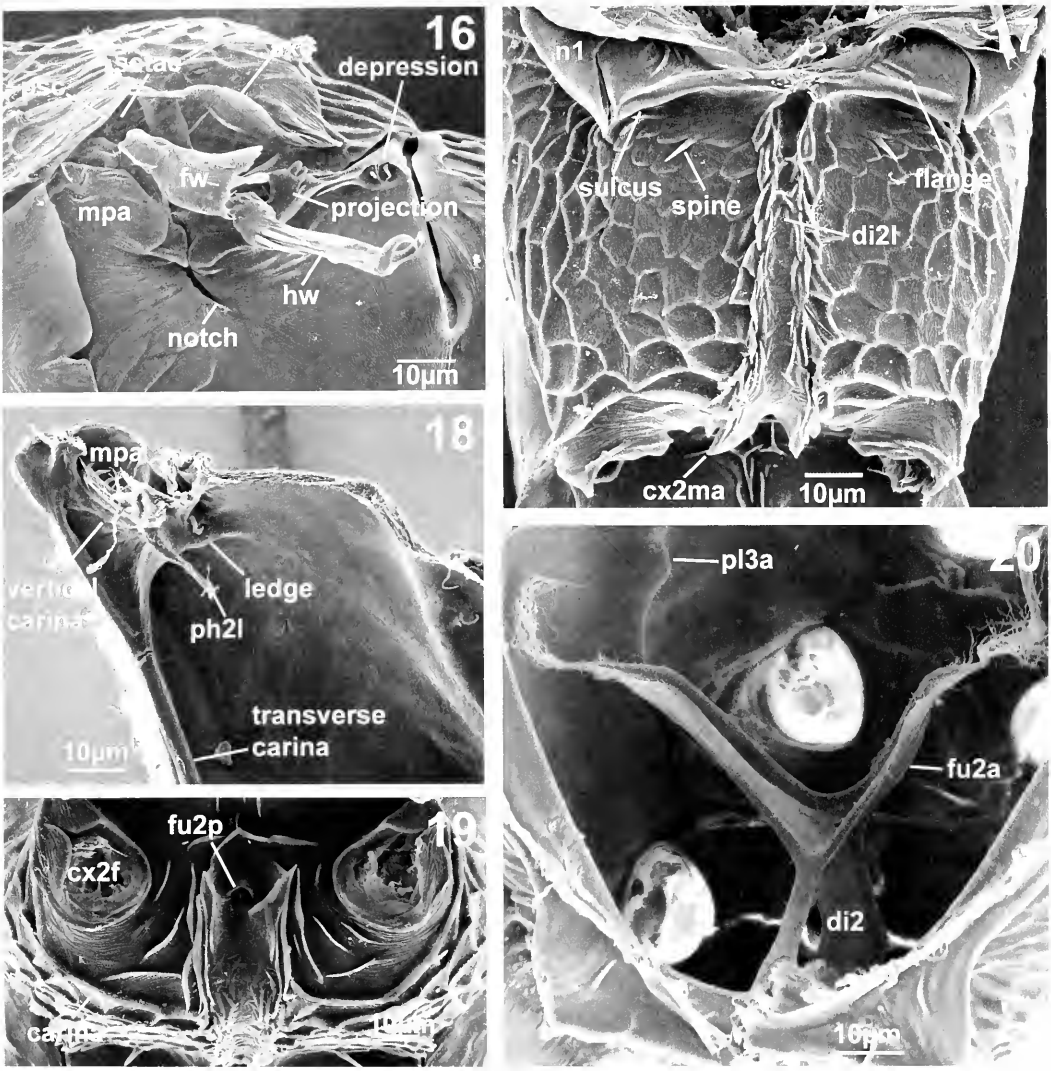
Figs 6–9. Propectus of *P. anomalum*. 6. Exterior ventral view; 7. Exterior anterior view. 8. Prosternum, posterior view (pronotum removed); 9. Profurca, dorsal view. Abbreviations: cep = cervical prominence; cx1 = procoxa; fu1 = profurca; fu1a = profurcal arm; fu1p = profurcal pit; pl2 = mesopleuron; st1 = prosternum; ppa = propleural arm; sp1: prospinasternum; te = tendon.

below parascutal carina just above fore wing base (Fig. 16). Tegula absent. Mesoscutellum with convex, reticulate anteromedian part between lateral depressed areas having more weakly developed sculpture, and with depressed, longitudinally striate posterior frenum (Figs 10, 11) anteriorly delimited by external frenal line (Fig. 10, frle); convex median part with elongate seta laterally, without evident scutoscutellar sulcus (Figs 10, 11); frenum with sublateral triangular extension overlapping metanotum dorsally (Fig. 11, n3). Mesoscutellum with axillar carina distinct laterally (Figs 11, 16, axc), the carina subdivided posteriorly into posterodorsal branch extending across mesoscutellar arm proximally and anteroventral branch extending to distal end of mesoscutellar arm (Fig. 11, sca); anteroventral branch of axillar carina with seta. Mesoscutellar arm evident dorsolaterally on mesoscutellum just anterior of frenum (Fig. 11, sca), and with anterolateral part of arm slightly overhanging fore wing base and terminating in slender vertical rod just anteriorly of hind wing base (Fig. 11, hw). Internally, mesoscutellum delimited by low mesoscutellar carina anterolaterally, the carina not continuous medially (Fig. 13, msc); surface spanned by extended septum penetrated by small oval fenestrum in middle (Fig. 13, fen) and with a convex line (Fig. 13, frli) corresponding to external frenal line delimiting oblong transverse impression posteriorly of fenestrum;



Figs 10–15. Mesonotum of *P. anomalum*. 10. Mesonotum, dorsal view. 11. Mesoscutellum and axilla, posterolateral view. 12. Mesoscutum, ventral view. 13. Mesoscutellum, ventral view. 14. Prophragma, anterolateral view. 15. Mesophragma, ventral view. Abbreviations: axc = axillar carina; axp = axillar phragma; fen = fenestrum; frle = external frenal line; frli = internal frenal line; hw = hind wing; msc = mesoscutellar carina; n3 = metanotum; ph1 = prophragma; prf = propodeal foramen; psc = parascutal carina; sca = mesoscutellar arm; tf = tonofibrillae; tsa = transscutal articulation; tsc = transscutal carina.

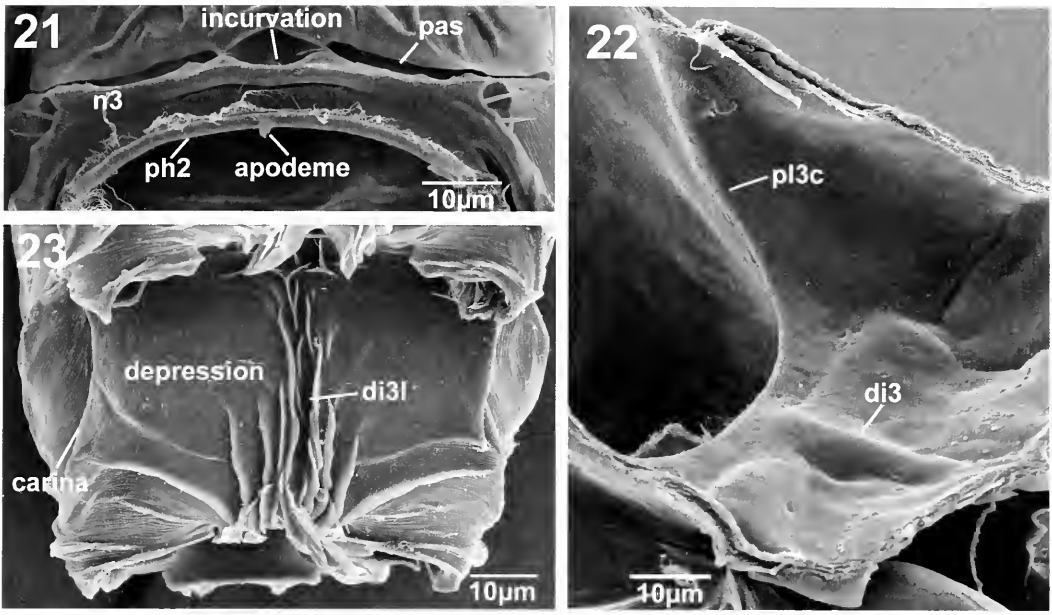
anteriorly with rod-like axillar phragmata (Figs 12, 13, axp) arising just posterior of transscutal articulation, the rods continuous medially along transscutal carina (Fig. 13, tsc) and projected anterolaterally, the projected parts inflected rather than flush with inner surface of mesoscutum (see discussion).



Figs 16–20. Mesopectus of *P. anomalum*. 16. Dorsal part of mesothorax, lateral view. 17. Ventral part of mesopleuron, ventral view. 18. Dorsal part of mesopleuron, internal view; 19. Posterior part of mesopleuron, posterior view. 20. Mesofurca, anterior view. Abbreviations: axc = axillar carina; cx2f = mesocoxal foramen; cx2ma = mesocoxal median articulation; di2 = mesodiscrimen; di2l = mesodiscrimenal line; fu2a = mesofurcal arm; fu2p = mesofurcal pit; fw = forewing base; hw = hind wing; mpa = mesopleural arm; n1 = pronotum; ph2l = mesolaterophragmal lobe; pl3a = metapleural apodeme; psc = parascutal carina.

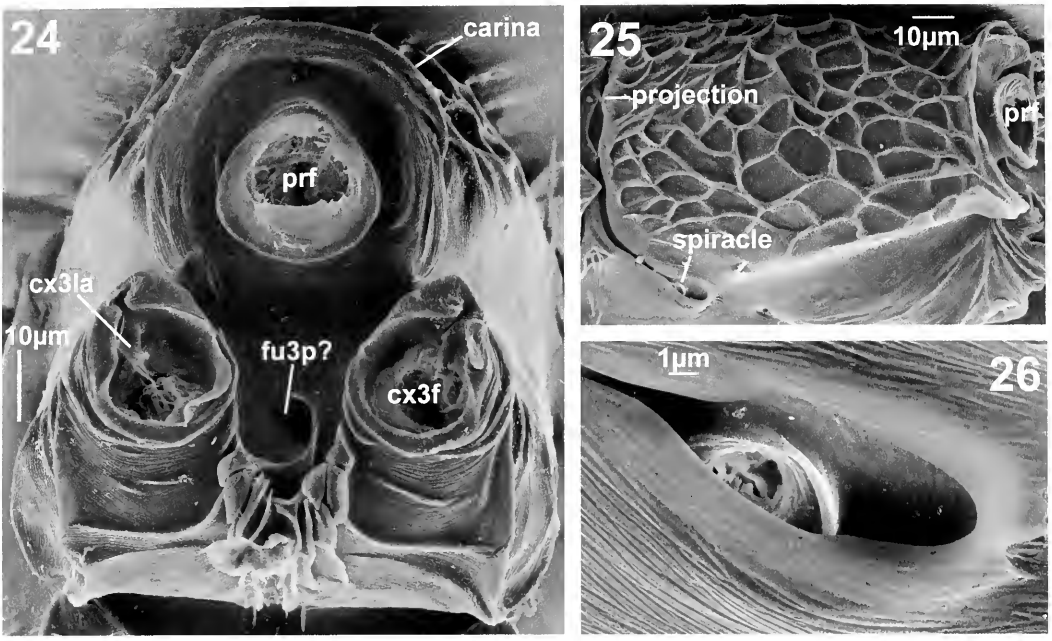
Mesophragma (Fig. 15) large, rectangular, extending far into propodeum almost to propodeal foramen; pseudophragmal lobes, ventral median longitudinal carina, and posterior median slit not developed, but with low, broad transverse swelling just posterior to anterior margin; anterior margin with tiny apodeme and associated tendon medially (Fig. 21). Laterophragmal lobes developed as slender, ventromedially projected rods on anterolateral extensions of mesophragma (Fig. 18, ph2l).

Mesopectus-metathorax-propodeum complex.—Mesopectus in anterior view with mesopleural margins forming U-shape, lateroventrally with triangular flange op-



Figs 21–23. Metathorax of *P. anomalum*. 21. Metanotum, anterodorsal view (dissected from mesothorax). 22. Ventral metapleuron, internal view. 23. Ventral metapleuron, external view. Abbreviations: di3 = metadiscrimen; di3l = metadiscrimenal line; n3 = metanotum; pas = propodeal antecostal sulcus; ph2 = mesophragma; pl3c = metapleural paracoxal carina.

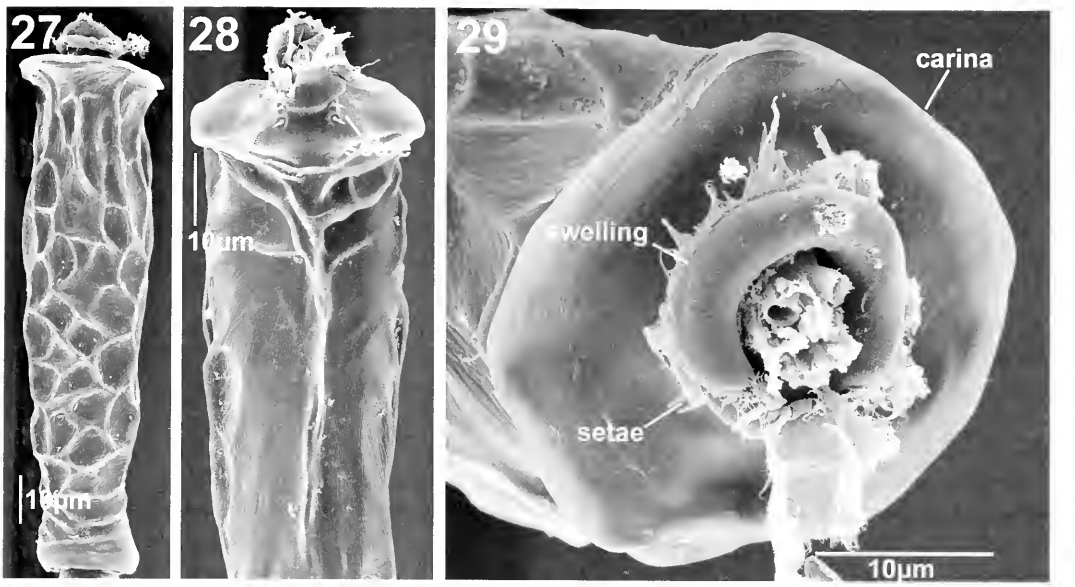
posite basal part of procoxa, the flange laterally articulating with posteroventral corner of pronotum (Fig. 17, n1). Mesopleura with transverse sulcus extending along entire anterior margin, internally the sulcus corresponding to low transverse carina extending onto mesopleural arms (Fig. 18). Prospinasternum present as very small area anterior to transverse carina, hardly visible in external view; internally, prospinasternal apodeme absent (Fig. 9, sp1). Mesopleural arm (Fig. 16, mpa) dorsally accommodating fore wing articulation, posteriorly delimited by distinct notch; internally, mesopleural arm supported by short, almost vertical carina, ventrally delimited by short horizontal ledge connected to anterior transverse carina (Fig. 18). Mesobasalare and posterior thoracic (metathoracic) spiracle neither observed internally nor externally. Mesopleuron with lateral surface reticulate anteroventrally, smooth posterodorsally (Fig. 1); ventral surface reticulate/scaly, with distinct spine anterolaterally (Fig. 17), and posteriorly with transverse carina delimiting smooth area around mesocoxal foramina (Figs 17, 19). Internally, mesopleural apodeme and mesepisternal ridge absent. Mesocoxal foramen (Fig. 19, cx2f) narrow, laterally overlapped by flange (Fig. 1) continuous with transverse carina; median mesocoxal articulation developed as short lobe (Fig. 17, cx2ma). Mesocoxa with proximal part (basicoxite) reduced. Mesodiscrimenal line (Fig. 17, di2l) a longitudinal smooth groove extending from anterior margin of mesopectus and terminating in mesopleural pit (Fig. 19, fu2p) between mesocoxal foramina. Internally, mesodiscrimen (Fig. 20, di2) anteriorly continuous with transverse carina; discrimen rising gradually to form high septum at point of origin of mesofurcal arms (Fig. 20, fu2a), then descending steeply to terminate in mesofurcal pit. Proximal part of mesofurcal arm slender, extending dorsolaterally, with shallow depression



Figs 24–26. Propodeum of *P. anomalum*. 24. Posterior view; 25. Dorsolateral view; 26. Propodeal spiracle. Abbreviations: cx3f = metacoxal foramen; cx3la = metacoxal lateral articulation; fu3p? = possible metafurcal pit; prf = propodeal foramen.

dorsally; anterior mesofurcal apodemes, mesofurcal bridge, and mesospinasternal apodeme absent.

Metanotum (Figs 11, 21, n3) a narrow transverse strip between anterior margin of mesophragma and antecostal sulcus; without developed metascutellum but posteriorly with slight median incurvation delimited by minute posterior projections and laterally with depression having two short setae (Figs 11, 16, 21). Metapleuron broad dorsally, accommodating hind wing in incurvation in thickened dorsal margin (Figs 1, 16). Small, triangular projection posteriorly of hind wing separated from bulk of metapleuron by narrow sulcus (Figs 11, 16); projection with small bilobed, possibly membraneous extensions posterodorsally. Metapleuron fused with mesopleuron for almost entire length laterally and ventrally (Fig. 1); separated from propodeum posterodorsally by antecostal suture (Fig. 1, pas), but fused with propodeum below propodeal spiracle, the boundary indicated by shallow groove extending from metapleural pit to notch just dorsal to metacoxal foramen (Fig. 1). Metapleuron with lateral surface smooth except for striate sculpture just anterior of metacoxal foramina and with small pit in middle (Fig. 1, pl3p) continuous with shallow paracoxal sulcus extending ventrally (Fig. 1, pcs); internally, metapleural pit corresponding to low apodeme (Fig. 20, pl3a) situated at dorsal end of low paracoxal carina extending across ventral part of metapleuron (Fig. 22, pl3c). Metapleuron with ventral surface smooth except for low longitudinal ridge of scaly projections formed along metadiscrimenal line (Fig. 23, di3l), the discrimenal line extending to circular depression (Fig. 24, fu3p?) between metacoxal foramina. Internally, circular depression corresponding to slight swelling, and metadiscrimen (Fig. 22, di3) developed as low longitudinal swelling reaching paracoxal carina; metafurca absent. Externally, metepisternal depression well developed laterally of metadiscrimenal line, laterally delimited



Figs 27–29. First petiolar segment of *P. anomalum*. 27. Dorsal view. 28. Ventral view of anterior part. 29. Anterior view.

by low longitudinal carina (Fig. 23). Metacoxal foramen (Fig. 24, cx3f) constricted, circular, surrounded by raised rim, separated from propodeal foramen by cuticle; median metacoxal articulation not developed, lateral articulation (Fig. 24, cx3la) concealed in lateral view.

Propodeum dorsally with scaly-reticulate sculpture anterior to transverse, semicircular carina above propodeal foramen (Figs 24, 25); bare except for long seta posterior to lateral end of antecostal suture (Fig. 1, pas); dorsally with minute submedian projection extending from anterior margin across antecostal suture to abut corresponding structure on metanotum (Fig. 25). Propodeal antecostal suture (Fig. 1, pas) a narrow transverse groove separating metanotum and propodeum (Figs 1, 21), the suture terminating laterally in small oval depression concealing propodeal spiracle (Figs 25, 26). Internally, propodeum with apodemes for spiracular muscles; metaphragma only observed laterally above propodeal spiracle, but median part might be indicated by presence of low transverse swelling anteriorly on mesophragma (Fig. 15; see above). Propodeal foramen (Fig. 24, prf) pear-shaped in outline, encircled by raised rim and surrounded by smooth cuticle; without distinct articulation process with metasoma.

Mesosoma-metasoma articulation.—Petiole two-segmented. First petiolar segment (predominantly abdominal T2, see discussion) slender, cylindrical, and dorsally reticulate (Fig. 27); anteriorly with portion articulating with propodeum constricted relative to rest of petiole (Figs 27, 28), its anterior margin swollen and circular in anterior view (Fig. 29); cuticle surrounding constricted portion smooth and posteriorly delimited by transverse carina encircling entire petiole (Figs 28, 29); anteroventrally with two sublateral setae on smooth surface posterior to anterior swollen margin (Figs 28, 29); with median longitudinal carina posterior to anterior transverse carina, but otherwise without conspicuous sculpture ventrally.

DISCUSSION

Debauche (1948) confused the lateral parts of the pronotum in *P. anomalum* with

the propleuron, stating that 'les propleures atteignent, en arrière, les insertions alaires' [p. 31: 'the propleura reach the wing articulations posteriorly']. Gibson (1986) clarified the configuration of the pronotum and its association with surrounding sclerites. The condition in *P. anomalum* differs from Chalcidoidea in that the pronotum is rigidly associated with the mesopleuron, a large exposed prepectus is absent (therefore the posterodorsal corner of the pronotum and the fore wing base are not widely separated), and there is no exposed spiracle situated dorsally between the pronotum and the mesoscutum.

The above statements require some qualification. A more or less rigid association of the pronotum with the mesopleuron and concurrent absence of an independent prepectus is widespread within the Apocrita and has probably evolved independently a number of times (Gibson 1985, 1999). A number of taxa (Cynipoidea, Platygastroidea, most Proctotrupoidea) have the prepectus fused to the posterior margin of the pronotum as the posterolateral pronotal inflection, forming an articulation with the mesopleuron. This condition is apparently not present in *P. anomalum*. Gibson (1986) could not establish the identity of the prepectus in Mymarommatidae with certainty, but suggested it to be homologous with the narrow internal carina extending vertically close to the posterolateral margin of the pronotum. Our findings support this; the carina survived treatment with KOH and hence must be cuticular, and a sclerite in this position would be the prepectus by default. Furthermore, the carina is apparently continuous with the pronotum, there being no indication of displacement of the structure due to shrinkage of membraneous cuticle (Fig. 4).

To further corroborate the identity of the prepectus, it would be desirable to establish the position of the anterior thoracic spiracle, which in most Hymenoptera is closely associated with the posterior margin of the pronotum anteriorly and the prepectus posteroventrally. An anterior thoracic ('mesothoracic') spiracle cannot be observed externally in *P. anomalum*. Gibson (1986) tentatively identified the spiracle in Mymarommatidae as a structure close to the posterolateral margin of the pronotum observed in a slide preparation, but was unable to confirm this with SEM investigations. Neither could we; the only internal structure observed close to the prepectus is a small pit just anterior to it (Fig. 4), and it likely is this pit that Gibson (1986) observed in the slide preparation. However, the pit is not associated with a tracheal trunk (unless the narrow tissue strands sometimes observed to issue from the pit are remains of this) or with an apodeme for a spiracle occlusor muscle. The plesiomorphic condition in Hymenoptera is that the spiracle occlusor muscle arises from the prepectus (Gibson 1985, Vilhelmsen 2000a). Consequently, *P. anomalum* apparently lacks a functional anterior thoracic spiracle.

Mymarommatidae also lacks a fore wing tegula according to Gibson (1986). Nevertheless, the condition in *P. anomalum* is not similar to that in most Chalcidoidea, in which there is broad contact between the mesoscutum and the exposed and dorsally expanded prepectus, which separates the tegula from the pronotum (a notable exception to this is the Rotoitidae, which have a slender, partially concealed prepectus; Gibson & Huber 2000). Even though the tegula is absent, the ventral part of the parascutal carina (Fig. 16, psc), which anteriorly delimits the concavity accommodating the tegula, extends anteriorly of the posterodorsal corner of the pronotum in *P. anomalum* (Fig. 16), like in virtually all Hymenoptera except Chalcidoidea, where the carina terminates well posteriorly of the corner. The configuration of the tegula and parascutal carina relative to the posterodorsal corner of the pronotum is correlated with the occurrence of a dorsally enlarged prepectus. In conclusion, the pres-

ence of a concealed prepectus not in contact with the mesoscutum in Mymarommatidae is plesiomorphic relative to Chalcidoidea, whereas the fusion of the prepectus to the pronotum is apomorphic, but paralleled in many other Apocrita (Gibson 1985, 1999). The absence of both tegulae and anterior thoracic spiracles are possibly autapomorphic for Mymarommatidae.

Another putative autapomorphy is the fusion of the medioventral margins of the propleura and the fusion of the prosternum to the propleura (Fig. 6). The boundary between the propleura and the prosternum is difficult to establish. The profurcal pit (Fig. 8, fu1p) is situated dorsally of the procoxal bases (Fig. 8, cx1); however, in most Hymenoptera the prosternum extends well ventrally of the pit before bending anteriorly above the propleura. We consider it most likely that the smooth areas medioventral to the procoxal bases are part of the prosternum (Fig. 8, st1) and the fusion with the propleura took place ventrally of these, just dorsally of the extended posteroventral margins of the propleura. Anteriorly, the boundary between the propleura and prosternum is even less obvious. The base of the profurca does not extend far anteriorly, indicating that the anterior part of the prosternum was short prior to fusion. However, those Chalcidoidea with an exposed, anteriorly extended prosternum also do not have the profurcal base extending far anteriorly (Vilhelmsen unpubl.; Krogmann unpubl.), so this feature is apparently of limited value in deducing the anterior limits of the prosternum.

In virtually all Chalcidoidea the medioventral margins of the propleura diverge posterolaterally to broadly expose an anteriorly extended, diamond-shaped prosternum (Krogmann 2005, Bucher 1948, fig. 18). In most other Hymenoptera, except for the basalmost lineages (Xyeloidea and Tenthredinoidea; Vilhelmsen 2000a), the medioventral margins abut for most of their length from just posteriorly of the cervical prominences to the posterior margin of the propleura level with the procoxal bases, and cover the anteroventral part of the prosternum if the latter is developed. Given that the Mymarommatoidea is the putative sistergroup of Chalcidoidea, it would be highly informative to know what the configuration of the prosternum was prior to its fusion with the propleura. Because of the difficulties with establishing the anterior boundary of the prosternum in *P. anomalum* (see above) it is not possible to determine this condition.

The fusion of the propleural and profurcal arms in *P. anomalum* (Fig. 9) is another putative mymarommatid autapomorphy and possibly correlated with the fusion of the prosternum and propleura. In other Hymenoptera, the lateral end of the profurcal arm articulates with the posterodorsal margin of the propleuron, an autapomorphy of the Hymenoptera (Vilhelmsen 2000a). The propleural-profurcal articulation perhaps forms a suspension for the fore legs. The fore legs articulate with the propleura and abut the prosternum. The propleural-profurcal articulation presumably allows the prosternum to become slightly displaced relative to the propleura, thus softening the impact of the legs on the substrate and dampening it before it is transmitted to the head. The fusion of the propleura and the prosternum in *P. anomalum* could have made the articulation redundant because the prosternum and propleura are immovable relative to one another. The profurcal bridge, a sclerotised connection between the opposite dorsal parts of the profurcal arms extending above the ventral nerve cord, is also missing from the majority of Chalcidoidea (Krogmann 2005). However, the occurrence of this feature is highly variable throughout the Apocrita (Vilhelmsen 2000a, unpublished observations).

The exposed cervical prominence at the anterolateral corner of the propleuron (Fig. 7, cep) is a feature shared by *P.*

anomalum and at least some Chalcidoidea (unpublished observations). In most other Apocrita, the cervical prominence is somewhat retracted and below the anterodorsal corner of the propleuron (Vilhelmsen 2000a). The condition in *P. anomalum* is perhaps correlated with miniaturization. The small number of sensilla (3) at the cervical prominence probably also is a consequence of small size; other, larger Hymenoptera, have up to 20–30 sensilla in this position on a prominent cervical swelling (Vilhelmsen 2000a, unpublished observations).

In *P. anomalum*, the dorsal posterolateral corner of the propleuron accommodates the posteroventral corner of the pronotum in a distinct groove (Figs 2, 8). This is not observed in any Chalcidoidea, where the pronotum is much less integrated with adjacent sclerites (see above). A similar condition to that in *P. anomalum* is possessed by most Ichneumonoidea (unpublished observations). No other features appear to link Ichneumonoidea with Mymarommatidae, so the condition in *P. anomalum* is probably independently derived and a further putative autapomorphy of Mymarommatidae.

The prophragma of *P. anomalum* differs from that of Chalcidoidea in not being subdivided medially by a slit and not extending laterally. The presence of a slit and the absence of a lateral extension of the prophragma are the plesiomorphic conditions, being common within Hymenoptera. Furthermore, the prophragma has rods extending from it dorsally (Fig. 14), which have not been observed in any other Hymenoptera. The function of these rods could not be ascertained, but it is likely they are apodemes that accommodate prophragmo-pronotal muscles; indeed, what appears to be tonofibrillae were in some instances associated with the rods (Fig. 14, tf). The position and configuration of the prophragmal rods might indicate that they are serial homologues of the axillar phragmata (see below), which arise just anteriorly of the mesophragma. Unlike the axillar phragmata, the prophragmal rods probably do not accommodate nototrochanteral muscles because pronoto/phragmal-protrochanteral muscles are absent from the Hymenoptera that have been examined for musculature, although pronotal-procoxal muscles do occur (Vilhelmsen 2000a). The presence of axillar phragmata remains the most convincing synapomorphy for Chalcidoidea and Mymarommatoidea (Gibson et al. 1999). The homology of the structures in the two taxa is based on the topology regarding muscle attachments and position relative to the surrounding structures. However, the configuration of the axillar phragmata is quite different from that of Chalcidoidea. In Chalcidoidea, the phragmata are flat, broad structures that usually lie adjacent to the internal part of the mesoscutum (Krogmann 2005). In *P. anomalum*, the phragmata are slender, cylindrical rods that are continuous medially through the transscutal carina (Fig. 13, tsc) and project away from the mesoscutum into the lumen of the mesosoma. The difference in structure and the possibility that in Mymarommatidae the axillar phragmata are serial homologues of the prophragmal rods, might indicate that they were independently derived from those of Chalcidoidea. Alternatively, the difference in structure of the axillar phragmata between Mymarommatidae and Chalcidoidea may reflect simple size differences in the tergo-trochanteral muscles or some other functional requirement.

The mesoscutum anteriorly of the transscutal articulation in *P. anomalum* is devoid of any external and internal features (mesoscutal sulcus, notauli, parapsides). Most apocritan wasps, including Chalcidoidea, have at least the notauli developed. The posterior border of the axilla in *P. anomalum* is delimited internally by the posterior margin of the axillar phragmata and the lateral mesoscutellar carina.

The transverse subdivision of the mesoscutellum into an anterior raised part

and a posterior depressed part (further emphasized by the difference in sculpture in *P. anomalum*, Figs 10, 11) is also observed in some Chalcidoidea (Krogmann 2005). In the Chalcidoidea, the posterior part is known as the frenum, and the dividing line as the frenal line. If the presence of a frenum is a ground plan feature of the Chalcidoidea, it might be an additional putative synapomorphy of Mymarommatidae and Chalcidoidea (Gibson et al. 1999). The identity of the frenum in Mymarommatoidea is corroborated by its relation to the mesoscutellar arms, the latter arising just anteriorly of the external frenal line (Fig. 10, frle) as in those Chalcidoidea having a frenum. Of the two branches of the axillar carina in *P. anomalum*, the anterior is probably homologous with the single carina in most other Hymenoptera, because it terminates at the anterior end of the mesoscutellar arm, the normal condition in taxa with only one branch.

The large, rectangular mesophragma with a straight posterior margin extending through most of the propodeum in *P. anomalum* is a feature also observed in some Mymaridae (e.g., *Gonatocerus*; unpublished observations). If Mymaridae are indeed basal within the Chalcidoidea (Gibson et al. 1999), this configuration of the mesophragma is putatively the ground plan condition for Chalcidoidea. Many Chalcidoidea have the mesophragma tapered posteriorly and with an incurvation in the posterior margin (e.g., Bucher figs 28–29), as do most Hymenoptera. The muscle arising from the apodeme medially on the anterior margin of the mesophragma (Fig. 21) is probably homologous with the mesoscutellar-metanotal muscle arising from the anterior margin of the metanotum in other Hymenoptera. Heraty et al. (1994) did not detail the condition in Mymarommatidae or report a similar configuration for any other taxa they examined; the muscle also inserts on the anterior margin of the mesophragma in *Xiphydria* (Xiphydriidae; Vilhelmsen 2000b).

The extensive fusion in the mesosoma forming the mesopectus-metathorax-propodeum complex is not unique for Mymarommatidae. Indeed, the fusion between the propodeum and posterodorsal part of the metapleuron is an autapomorphy for the Apocrita (Vilhelmsen 2000b). Within the Apocrita several taxa have the meso- and metapleura fused to varying degrees, but only in Mymarommatidae and Ceraphronoidea are they fused along almost their entire common boundary (Vilhelmsen unpublished). The integration in Ceraphronoidea has gone even further, because the dorsal and ventral parts of the metathorax have become almost entirely reduced. In Chalcidoidea, the meso- and metapleura closely abut, as in all Apocrita, but usually are not fused.

The pronounced integration and general scarcity of anatomical reference points in the mesopectus-metathorax-propodeum complex means that the boundaries between the constituent parts can only be loosely established. The following anatomical features are relevant for this exercise: the fore and hing wing bases, the lateral ends of the metathorax, the metapleural pit, the propodeal antecosta and spiracle, the meso- and metacoxal cavities and lateral articulations, the meso- and metafurcal pits, and the propodeal foramen.

The lateral boundaries between the meso- and metapleuron and the propodeum are indicated in Fig. 1. The dorsal endpoint of the boundary between the meso- and metapleuron can be identified at the bottom of the slit that separates the fore- and hind wing bases (Fig. 16). The posterior thoracic spiracle would have provided a useful landmark, but is apparently absent, as in many apocritan wasps, including Chalcidoidea (unpublished observations). Posteroventrally, the boundary between the meso- and metapleuron probably lies just anteriorly of the metapleural paracoxal sulcus, which extends as a verti-

cal groove from the metapleural pit to the notch above the mesocoxal foramen (Fig. 1). Ventrally, the boundary between the two regions is more easily identified by the groove that extends between the notches above the mesocoxal foramina and the mesofurcal pit (Figs 19, 23). The mesofurcal pit lies between the coxal foramina, not anteriorly of them as in almost all Chalcidoidea; the anterior position of the mesofurcal pit is a putative autapomorphy of the Chalcidoidea. A transverse carina is present just anteriorly of the mesocoxal foramina and pit as in Chalcidoidea, but also in some other Apocrita.

The mesofurca in *P. anomalum* is comparatively simple, lacking a mesofurcal bridge or any conspicuous apodemes (Fig. 20). The mesofurcal bridge is also absent from some Chalcidoidea, notably putatively basal taxa such as Mymaridae and Rotoitidae. This was noted by Heraty et al. (1997), but because of its widespread occurrence in Apocrita they considered the presence of a bridge to be the ground plan state for Chalcidoidea. The proximal part of the mesofurcal arm is only slightly depressed in *P. anomalum*. In most Chalcidoidea, a distinct dorsal concavity is developed to various extents in this region, a putative autapomorphy for the superfamily.

The boundary between the metathorax and propodeum is comparatively easy to establish, at least dorsally, being marked by the antecostal suture (Fig. 1). The putative boundary then extends between the lateral end of the suture and the metapleural pit towards the metacoxal lateral articulation along a shallow groove (Fig. 1). Posteriorly, the boundary extends between the metacoxal and propodeal foramina (Fig. 24). Apparently, the lateral part of the metapleuron is expanded dorsally and ventrally, but constricted near the metapleural pit (Fig. 1).

The metanotum is reduced in comparison to most other Hymenoptera, but is still identifiable. No distinct features (e.g., metascutellum) are evident (Figs 11, 21) other than the two small submedian projections that extends across the antecostal suture to abut similar, anteriorly projecting structures on the propodeum. Such structures are absent from Chalcidoidea (unpublished observations), but they might be homologous with those observed in many Proctotrupoidea, Cynipoidea, and Ichneumonoidea.

The function of the triangular projection posteriorly of the hind wing and the bilobed extensions it accommodates (Figs 11, 16) is unknown; the extensions may possibly serve as sensillae monitoring the movements of the hind wing base. It is also unclear whether the extensions are membraneous; if they are, their bilobed configuration is possibly an artifact.

Internally, the metapleuron has a low internal swelling (Fig. 20, pl3a) that corresponds to the metapleural pit (Fig. 1, pl3p) and which is apparently the reduced metapleural apodeme. The low carina extending between the apodemes is the paracoxal carina, usually situated along the anterior margin of the metapleura (Fig. 22, pl3c); this configuration of the apodeme and carina is widespread in Apocrita. The metafurca is usually closely associated with the paracoxal carina, the metafurcal arms arising medially at the anterior end of the metafurcal discrimen (Vilhelmsen 2000b). In *P. anomalum*, the only remnant of the metafurca is the median depression between the metacoxal foramina (Fig. 24, fu3p?), which probably corresponds to the metafurcal pit, and a low longitudinal swelling (Fig. 22, di3) that corresponds to the metafurcal discrimen. The entire absence of metafurcal arms is a putative autapomorphy for the Mymarommatidae. In Chalcidoidea, there is substantial variation in the configuration of the metafurcal arms and the number and configuration of the metafurcal pits (Krogmann 2005). Unfortunately, the absence of the former structure in Mymar-

ommatidae makes it difficult to interpret the evolution of this structure within Chalcidoidea.

The accommodation of the propodeal spiracle within the lateral ends of the antecostal suture (Fig. 26) is also observed in *Trichogramma* (Krogmann 2005), but not outside Chalcidoidea. A more comprehensive survey of the occurrence of this trait within Chalcidoidea is required to establish its possible phylogenetic significance. The presence of well developed apodemes internally of the spiracle indicates that it is the only functional spiracle in the mesosoma of *P. anomalum*.

The slender, two-segmented petiole is only observed in the extinct taxon Serphitidae apart from in Mymarommatidae; based on this, it has been hypothesized that they form a monophylum (cf. Gibson 1986). The first petiolar segment of *P. anomalum* essentially is a narrow, sclerotised tube with little indication of boundaries between individual sclerites. This condition occurs in many Apocrita, including some Chalcidoidea, and is difficult to interpret. The ventral longitudinal carina extending along most of the first petiolar segment in *P. anomalum* is perhaps formed by the fusion of the lateral margins of the second abdominal tergum (T2), indicating that T2 is expanded ventrally and the sternum of this segment is reduced or absent (Gibson in litt.). However, the setae situated anteroventrally just posterior to the anterior margin of the first petiolar segment (Figs 28, 29) are probably homologous with the sensillar patches situated sublaterally on S2 in Apocrita that have this sclerite separate from T2. This indicates that at least the anteriormost part of S2 is present in *P. anomalum*. The continuous transverse carina anteriorly on the first petiolar segment (Fig. 29) is also observed in many Proctotrupoidea, Cynipoidea, Platygastroidea, Ceraphronoidea as well as in some Chalcidoidea (unpublished observations).

CONCLUDING REMARKS

The present study underlines the highly autapomorphic status of the Mymarommatidae. However, we have only examined *P. anomalum*, and the features we have studied need to be surveyed for a larger sample of the family. According to Gibson et al. (1999), the diversity of Mymarommatidae is not sufficiently reflected by the current classification that has all extant species lumped in *Palaeomymar*, a situation that will probably change once the family has been comprehensively revised. Given the small size of all Mymarommatidae and that it possibly occupies a key phylogenetic position within Apocrita, detailed morphological studies of additional species are recommended to test our inferences.

Many of the putative autapomorphies of Mymarommatidae are reductional and probably correlated with miniaturization (e.g., the absence of the anterior thoracic spiracle and the metafurca). Furthermore, being morphologically highly derived and isolated confounds attempts to homologize features with those in other Apocrita (e.g., the extensive fusion in the propectus, the difficulties in establishing the identity and configuration of the prepectus). The sistergroup relationship to the Chalcidoidea (also a highly autapomorphic taxon) seems the best supported hypothesis at present, but may prove difficult to corroborate further from morphological evidence alone. Mymarommatidae has not been represented in any phylogenetic analyses of Hymenoptera including molecular data, not even the most recent comprehensive ones (Campbell et al. 2000, Dowton and Austin 2001). Sequence data might confirm or challenge current concepts of the phylogenetic affinity of these intriguing animals.

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Nesting Biology of a Tropical Myrmicine Ant, *Myrmicaria arachnoides* (Formicidae), in West Java, Indonesia

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Abstract.—Nesting biology of a myrmicine ant, *Myrmicaria arachnoides*, was studied on Java island, Indonesia. The colonies were polydomous and polygynous. Nests of a colony were located close to each other on different leaves of a tree. The number of dealated queens was positively correlated with the numbers of nests, adult workers and immatures, but not with the numbers of males and new queens present. Adaptive aspects of nesting site, polygyny and polydomy are discussed.

The genus *Myrmicaria* is widely distributed in the Old World tropics, i.e., Southeast Asia, South Asia and tropical Africa. Emery (1922) sorted *Myrmicaria* species into two principal groups based on morphology, i.e., the *M. brunnea* group and *M. arachnoides* group, and briefly mentioned that species of the former construct huge nests underground while those of the latter construct carton nests on trees. Our observations have confirmed this for most of the Southeast Asian forms (also see Karavaiev 1935). However, there are few detailed studies on the nesting habits of *Myrmicaria*. In Cameroon, Africa, one species, *M. opaciventris* Emery, belonging to the *M. brunnea* group, has been intensively studied for its ecology/bionomics including nesting habits (Kenne and Dejean 1999, Kenne et al. 2000, 2001). This species has polydomous and polygynous colonies in the soil. Interconnected nests are built and trenches and tunnels are constructed as underground trails connecting nests. Species of the *M. arachnoides* group also often construct polydomous and polygynous colonies but on vegetation (Karawajew 1935, this study, Bakhtiar and Yamane unpubl.). This may allow them to develop relatively large colonies similar to *Polyrhachis* species nesting in similar situations (R. Kohout pers. com.).

Research on colony growth in eusocial insects has focused on the relationship between colony size and productivity. At each growth period, colonies make investment decisions about whether to produce more workers and grow larger, or rather to invest that energy in reproductive output (Billick 2001). Because colony size is often the most important factor determining reproductive output (Odum and Pontin 1961, Michener 1964, Fowler 1986, Tschinkel 1993, Savolainen et al. 1996), maximizing the long-term size of the colony is an important component of colony fitness (Oster and Wilson 1978). Colony size is known to be related with queen number and also to affect caste/sex composition in ant nests. In this respect nesting behaviour of the *M. arachnoides* group is of special interest.

Little has been studied on the colony structure of the Southeast Asian *Myrmicaria arachnoides* F. Smith (but see Karavaiev 1935). During our study on the taxonomy of Oriental *Myrmicaria* we obtained relatively good samples of *M. arachnoides* colonies on Java island, Indonesia. We report here the nesting sites, colony size, and reproductive output of these colonies.

MATERIALS AND METHODS

The taxonomy of *Myrmicaria* is still unresolved, particularly the status of infraspecific forms of some species. *Myrmicaria arachnoides* was originally described from Borneo and consists of several 'subspecies' (Bolton 1995), of which at least some would be good species. The form studied here is in coloration most similar to '*M. arachnoides arachnoides*'.

Samples were collected from three disturbed sites in West Java in September 2004: foot of G. Salak – Site 1 (6°39′ S, 106°46′ E, 560 m) (BOG3, 10 & 18), Salak-Halimun Corridor – Site 2 (6°45′S, 106°37′E, 710 m) (BOG24, 25 & 26), and Bogor Botanical Garden – Site 3 (6°36′S, 106°48′E, 220 m) (BOG 38). The distance between each plant where these colonies were found was approx. 5–50 m in Site 1, and 5–10 m in Site 2. These habitats have been infringed by plantation or agricultural activities or surrounded by residential areas. Nests constructed on a same plant were thought to constitute a single colony as the ants use same foraging trails. Nests of each colony from different plants were collected intact and put into plastic bags separately. In total, seven colonies of different sizes were collected.

Nests were measured for their maximum width and length, and then dissected carefully. Workers, reproductives (dealated queens, young winged queens and males), immatures (eggs, larvae and pupae) were counted and preserved in 80% alcohol. Pupae were sorted into sexes and castes as much as possible.

RESULTS

Nesting site and structure.—In Salak and Salak-Halimun Corridor, colonies were found in plantation areas with sparse trees and bushes, while in the botanical garden they were found in a forested area with relatively high trees. Nests were located on the underside of leaves of various plant species at 0.5–1.5 m above the ground in the former two sites (Fig 1 a,b), but in the botanical garden they were positioned higher at around 3–4 m above the ground. In the case of polydomous colonies component nests were generally constructed separately on different leaves of the same plant, but in one case, two nests were built narrowly connected on one and the same leaf (BOG25-2 & -4) (Appendix 1).

Nests were made of carton-like material (probably chewed plant tissues), flattened domes in shape, and greyish brown in colour. Various sizes of nests were built on the underside of various sizes of leaves (Appendix 1). Within the nest, there were numerous chambers for adults and immatures; some of these would be used as galleries for the movements of workers (Fig. 1 b,c).

The number of nests per colony varied from 1 to as many as 12; nests of a colony were usually built close to each other on one plant (approx. 15–30 cm apart).

Colony composition.—Dealated queens (Q) were considered to be foundresses or those that have joined later (simply called 'queens' hereafter) and were found in all colonies and all nests except in BOG18-3 and BOG25-11. The two queenless nests had immatures, suggesting the transportation of them from other nests where a laying queen(s) existed. The number of queens differed from colony to colony and nest to nest (Fig. 2). Number of queens is highly correlated with the number of nests (Fig. 3a). The highest mean number of queens per nest, 11.67, was found in a 3-nest colony (BOG18) (range: 0–22) (Fig. 2). However, BOG38 which also had 3 nests had the smallest number of queens in each of the

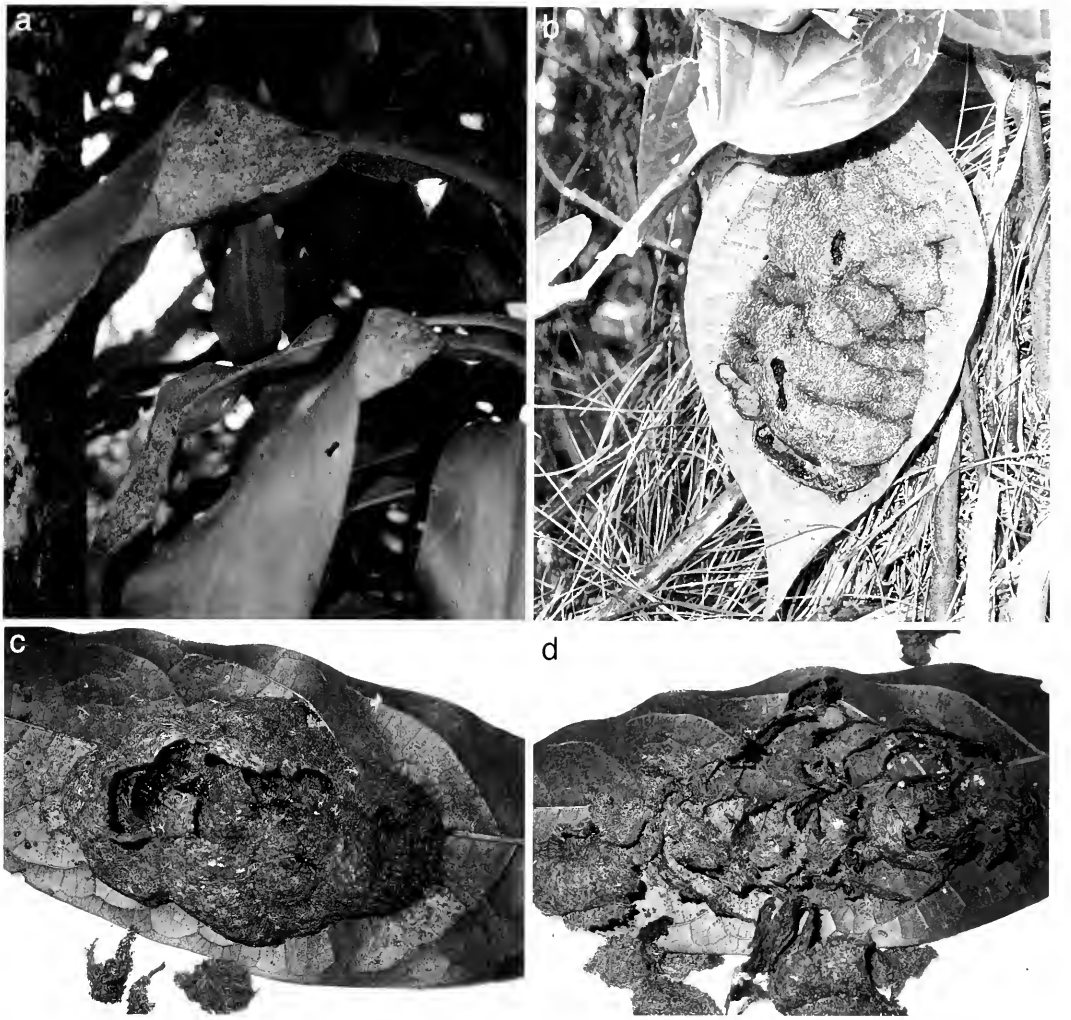

Fig. 1a–d. a, Nests constructed on underside of leaves. b, Nest on the underside a leaf. c, Structure of a nest; top of envelop removed to show the interior. d, Compartments within nest; outer walls removed.

nests (mean=1.33 with a range of 1 to 2). BOG24 (1-nest colony) and BOG3 (2-nest colony) contained relatively small numbers (1–3) of queens per nest. In larger colonies, BOG10 (4-nest colony) and BOG25 (12-nest colony), the mean number of queens per nest was larger and relatively stable (4.00 ± 2.16 & 4.00 ± 3.34 respectively).

Within each colony, workers represent the greatest number among inhabitants (approx. 40%) except in BOG 25 and BOG26 (approx. 30.3%), followed by eggs (approx. 20–40%) and larvae (approx. 10–30%). Worker pupae and male adults constitute relatively lower ratios, while other life forms (stages) were much fewer.

Most of the nests had queen(s), workers and immatures, and there was no striking specialization for a certain nest(s) in a single colony with respect to worker/reproductive production. However, BOG18-3, BOG38-1, BOG26-3 and BOG10-2 contained higher percentages of workers compared with other nests composing these colonies (Appendix 1).

In the single 1-nest colony (BOG24), all the adults were workers (approx. 40% of all the inhabitants) except for three queens

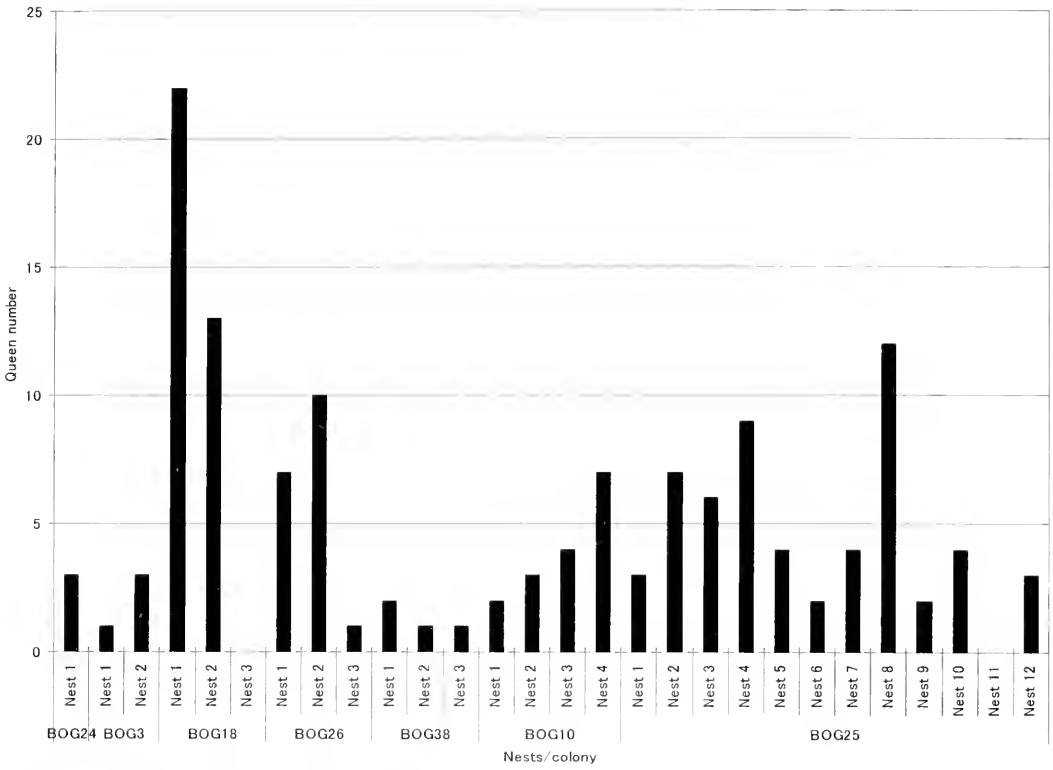

Fig. 2. Number of queens in each nest and colony.

that were possibly egg layers. There were numerous eggs (approx. 45%), while larvae and pupae were relatively few, being approx. 10% and 5%, respectively. Furthermore, all the pupae were workers, all this suggesting that the colony was in its ergonomic stage (reproduction and dispersal are not its immediate concern) (cf. Oster and Wilson 1978).

In the single 2-nest colony (BOG3) all life stages were present except the pupae of new queens (Appendix 1). Males had started to be produced, representing approximately 5% of the total adults for the colony (Appendix 1). Male pupae also existed in BOG3-1 (Appendix 1). Adult workers, eggs and larvae each had similar percentages for the whole colony and also for each component nest.

In the three 3-nest and 4-nest colonies (BOG18, 26 and 38), all life stages were present except the pupae of new queens (in all colonies), and winged adult queens in colony BOG26 (Appendix 1). As in smaller colonies mentioned earlier, workers again constitute between 30 and 40% of all inhabitants. Following the workers, eggs and larvae also occupied large proportions except in BOG18-3, just as in the smaller colonies. In BOG18-3, more adult males were observed. Worker pupae were observed to constitute approximately 5% in the colonies BOG38 and BOG26.

In the 12-nest colony (BOG25; Appendix 1), winged queens were seen only in two nests in small numbers, while males were distributed more evenly; the pupae of new queens were absent in this colony. For the whole colony, workers, eggs and larvae had approximately the same numbers (around 30%) while approximately 10% were worker pupae.

Reproductive output.—There were strong relationships between the number of

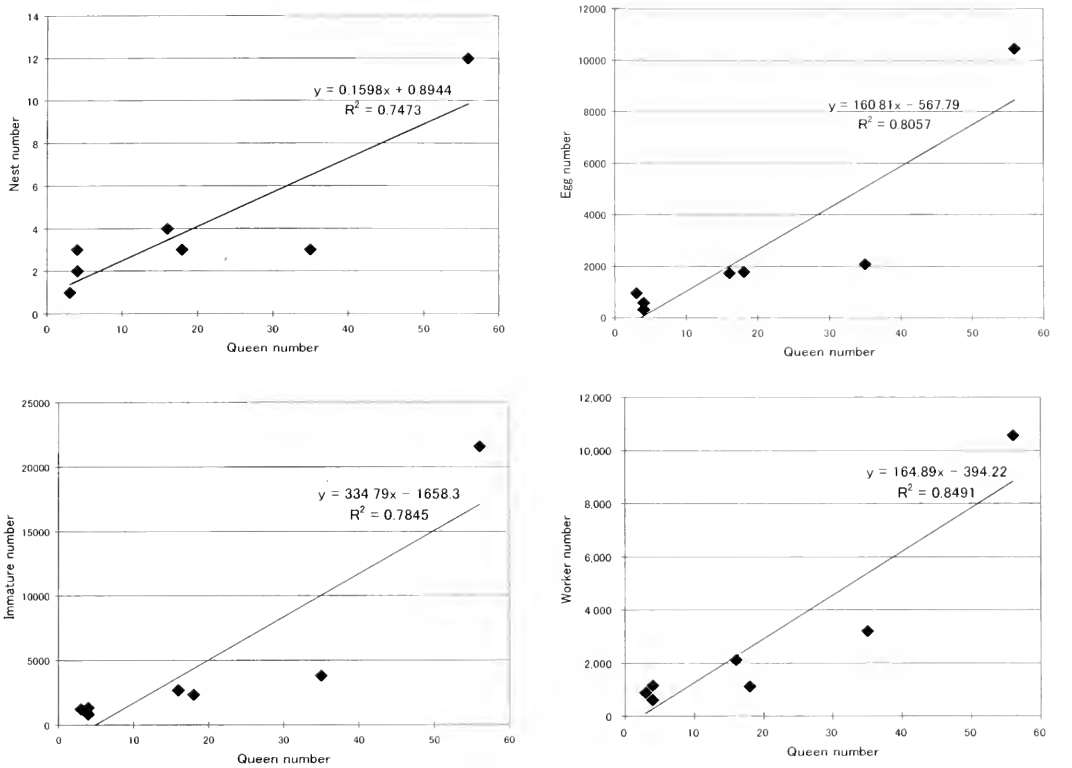

Fig. 3a–d. a, Correlation between queen and nest numbers. b, Correlation between queen and egg numbers. c, Correlation between queen and immature numbers. d, Correlation between queen and worker numbers.

queens and those of workers and immatures (Figs 3 b–d) (but the correlation was often strengthened by the values for the largest colony BOG25). These relationships sometimes hold also among the nests of single colonies but usually with a smaller R^2 as seen in BOG10 and BOG25 (R^2=0.0577 and 0.5549 respectively). In BOG38, however, the relationships were negative. Egg:worker ratio was relatively constant with a mean of 0.86 ± 0.5 and 0.88 ± 0.39 for each nest and colony respectively (Table 1). Number of queens was not significantly correlated with the numbers of new queens and males found in every colony (R^2=0.0919 and 0.0254 respectively).

DISCUSSION

Nesting site, nest structure and adaptation to arboreal nesting.—We found nests of *Myrmicaria arachnoides* in small remnant patches of secondary forests surrounded by human settlements and plantations, and colony/nest density was relatively high. However, not all such patches harboured this ant. Generally, nests are built of carton on the under-surface of leaves with 1–2 entrances in the outer envelope. This nesting habit may protect the nests from rain and visual predators; see Hölldobler and Wilson (1990) for other adaptive features of arboreal nests. Several colonies were found to be located close to each other but on different trees (approx. 5–10 m). Closer observations, both behavioral and genetic, are needed to clarify if they are completely independent from each other or form a kind of supercolony.

Polygyny and polydomy.—*Myrmicaria arachnoides* colonies observed in the present study clearly showed a polydomous and polygynous condition. At present it is not

Table 1. Egg:worker (E:W) ratio.

Colony	Nest	E:W ratio for nest	E:W ratio for colony	Colony	Nest	E:W ratio for nest	E:W ratio for colony
BOG24	BOG24	1.08	1.08	BOG25	BOG25(1)	1.00	0.99
BOG3	BOG3(1)	0.47	0.50		BOG25(2)	1.15	
	BOG3(2)	0.53			BOG25(3)	0.88	
BOG18	BOG18(1)	0.65	0.65		BOG25(4)	1.28	
	BOG18(2)	0.66			BOG25(5)	0.86	
	BOG18(3)	0.00			BOG25(6)	0.85	
BOG26	BOG26(1)	1.98	1.59		BOG25(7)	1.02	
	BOG26(2)	2.00			BOG25(8)	1.38	
	BOG26(3)	0.37			BOG25(9)	0.22	
BOG38	BOG38(1)	0.22	0.50		BOG25(10)	0.73	
	BOG38(2)	1.37			BOG25(11)	0.71	
	BOG38(3)	0.69			BOG25(12)	0.82	
BOG10	BOG10(1)	1.73	0.82				
	BOG10(2)	0.23					
	BOG10(3)	0.61					
	BOG10(4)	0.69					
	MEAN	0.86 ± 0.5	0.88 ± 0.39				

known whether polygyny in the present case was the result of pleometrosis (colony foundation by multiple queens) or later joining of inseminated daughters or alien females, and whether all the queens are egg layers or not. But the distribution of queens and immatures in colonies strongly suggests the existence of multiple egg layers.

Ecological factors have been invoked to explain the emergence of polygyny, in particular, high dispersal risks, high probabilities of colonies losing their queens, short queen lifespan compared to colony survivorship and low success of individual queens conducting independent colony founding (Keller 1995, Elias et al. 2005). Sudd and Franks (1987) also reasoned that queens may come together at the colony-founding stage to pool their resources during the first and most vulnerable stages in colony growth (for the advantage of pleometrosis, see also Hölldobler and Wilson, 1990).

The presence of multiple queens in nests and colonies in most of the samples studied here can be discussed in relation to nesting site and competition with other species. As mentioned above, nesting of this species (and probably of its related forms) is found in rather restricted patches of suitable habitat, but usually in high densities in the patches where they have established themselves. Successful establishment of immigrant queens may be not common, but accomplished by rapid development of colonies helped by pleometrosis and polygyny, and surviving populations will be maintained by polydomy and adoption of additional queens (for *Camponotus*, see Hansen and Klotz 2005). Thus, trees of a certain area can be dominated by this species as observed in Salak-Halimun Corridor. Although the ant fauna associated with *M. arachnoides* is not yet known, the above reasoning does not contradict the "ant mosaic" mentioned by Majer (1993), Djieto-Lordon and Dejean (1999), and others.

In polygynous colonies of *Myrmicaria arachnoides*, there is a possibility of colony reproduction due to budding (cf. Elias et al. 2005). In this case there should be a polyethism among new queens: some disperse to other patches after mating flights, and others prefer to move to nearby branches

or trees with a group of workers. However, we do not have any evidence supporting this view.

Colony size and reproductive production.— Smaller colonies (eg. BOG24) obviously had lower numbers of inhabitants (Appendix 1). These may have been at stages just after the colony foundation (cf. Sudd and Franks 1987). Data for other colonies show that as a colony grows in terms of the number of nests per colony, the number of colony members increases dramatically (Appendix 1), as suggested by Oster and Wilson (1978). In this subsequent stage, profits are mainly re-invested in workers and infrastructure such as the nest (Sudd and Franks 1987).

At some critical size, a colony begins to produce sexual offspring in order to realize its inclusive fitness. In our case even the 2-nest colony had already produced some males. But there was no relation between the colony size and number of males present. For example, in the 12-nest colony (BOG25), the number of males was relatively small as compared with BOG38 and BOG10 with fewer nests. Several factors may be responsible for this. Some males might have already left the nest when it was collected. Furthermore we do not know whether males are produced throughout the year or during restricted seasons.

The increase in queen number may increase the size of the colony, and finally the number of reproductives. Although in this study queen number positively affected the number of workers and immatures, the relationship between queen number and new queen (also male) number was not positive. This shows that other factors may have operated in determining the development of queens and males as reported for many other genera (for the Argentine ant, see Aron et al. 2001). In *M. arachnoides* maintaining a large worker force on one tree itself may be important under certain conditions (e.g., presence of competitors) at the cost of producing more reproductives. Furthermore we cannot know how many reproductives have been produced in a colony at the time of collection because dispersed individuals do not leave any indication of their previous presence in the colony unlike the case for social vespids where reproductive production can be measured rather precisely by observing pupal remnants.

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Appendix 1. Composition of life forms (stages) in colonies and nests.

	Nest	Nest & Leaf Measure	W	Q	WQ	M	Egg	Larva	WorkerP	MaleP	QueenP	Total
BOG24	Nest 1	N:5.0×7.5 cm L:7.7×24.5 cm	880	3	0	0	954	209	81	0	0	2127
BOG3	Nest 1	N:5.0×11.0 cm L:5.5×16.9 cm	549	1	2	38	257	390	7	4	0	1248
	Nest 2	N:7.0×12.0 cm L:10×17.0 cm	607	3	2	58	324	359	1	0	0	1354
	Subtotal		**1156**	**4**	**4**	**96**	**581**	**749**	**8**	**4**	**0**	**2602**
BOG18	Nest 1	N:14.5×16.0 cm L:22.0×28.0 cm	1780	22	38	69	1156	1039	1		0	4105
	Nest 2	N:10.0×14.5 cm L:26.0×27.5 cm	1413	13	14	86	929	657	39	5	0	3156
	Nest 3	N:NR L:NR	15	0	0	2	0	0	0	0	0	17
	Subtotal		**3208**	**35**	**52**	**157**	**2085**	**1696**	**40**	**5**	**0**	**7278**
BOG26	Nest 1	N:5.5×9.5 cm L:8.2×23.5 cm	415	7	0	6	820	214	91	1	0	1554
	Nest 2	N:4.5×8.8 cm L:6.0×17.0 cm	436	10	0	1	871	187	32	1	0	1538
	Nest 3	N:3.8×6.0 cm L:5.8×18 cm	278	1	0	3	104	43	1	0	0	430
	Subtotal		**1129**	**18**	**0**	**10**	**1795**	**444**	**124**	**2**	**0**	**3522**
BOG38	Nest 1	N:5.0×9.5 cm L:10.3×29.2 cm	335	2	3	36	75	61	17	12	0	541
	Nest 2	N:3.2×6.3 cm L:5.7×17.5 cm	62	1	0	6	85	105	9	2	0	270
	Nest 3	N:5.5×7.5 cm L:7.5×19.0 cm	212	1	0	20	147	274	44	6	0	704
	Subtotal		**609**	**4**	**3**	**62**	**307**	**440**	**70**	**20**	**0**	**1515**
BOG10	Nest 1	N:7.8×11.0 cm L:NR	417	2	3	64	719	295	69	1	0	1570
	Nest 2	N:6.0×9.0 cm L:NR	256	3	6	11	58	31	0	0	0	365
	Nest 3	N:6.0×12.0 cm L:3.5×16.0 cm	489	4	3	108	299	186	48	3	0	1140
	Nest 4	N:8.0×11.5 cm L:6.5×16.0 cm	956	7	11	139	661	312	14	0	0	2100
	Subtotal		**2118**	**16**	**23**	**322**	**1737**	**824**	**131**	**4**	**0**	**5175**
BOG25	Nest 1	N:5.5×14.0 cm L:7.5×36.5 cm	655	3	0	6	658	746	186	1	0	2255
	Nest 2	N:8.0×20.0 cm 6.0×16.5 cm L:9.0×48.0 cm	1380	7	0	12	1586	1260	339	3	0	4587
	Nest 3	N:6.0×26.0 cm L:9.5×34.5 cm	1259	6	1	7	1107	1100	363	3	0	3846
	Nest 4	N:6.5×20.0 cm L:9.5×31.cm N:5.0×12.5 cm L:7.0×18.0 cm	1437	9	0	6	1843	1545	321	7	0	5168
	Nest 5	N:6.5×16.0 cm L:9.5×44.0 cm	534	4	1	34	461	214	63	0	0	1311
	Nest 6	N:6.0×17.0 cm L:12.0×30.5 cm	714	2	0	1	610	503	157	0	0	1987

Appendix 1. Continued.

Nest	Nest & Leaf Measure	W	Q	WQ	M	Egg	Larva	WorkerP	MaleP	QueenP	Total
Nest 7	N:5.3×18.5 cm L:9.5×40.5 cm	617	4	0	0	632	224	120	2	0	1599
Nest 8	N:7.0×19.0 cm L:9.4×32.0 cm	1205	12	0	14	1658	1613	138	5	0	4645
Nest 9	N:5.5×14.5 cm L:8.5×27.0 cm	413	2	0	1	91	528	63	0	0	1098
Nest 10	N:6.5×12.5 cm L:7.8×20.5 cm	662	4	0	2	481	393	45	0	0	1587
Nest 11	N:6.0×16.0 cm L:9.3×36.0 cm	722	0	0	1	516	455	121	2	0	1817
Nest 12	N:7.0×19.0 cm L:9.8×28.5 cm	968	3	0	3	794	460	194	2	0	2424
Subtotal		**10566**	**56**	**2**	**87**	**10437**	**9041**	**2110**	**25**	**0**	**32324**

W=worker, Q=queen, WQ=winged queen, M=male, WorkerP=worker pupa, MaleP=male pupa, QueenP=queen pupa, NR=not recorded, N=nest, L=leaf.

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The Species of *Sternaulopius* Fischer (Hymenoptera: Braconidae, Opiinae) and the Braconid Sternaulus

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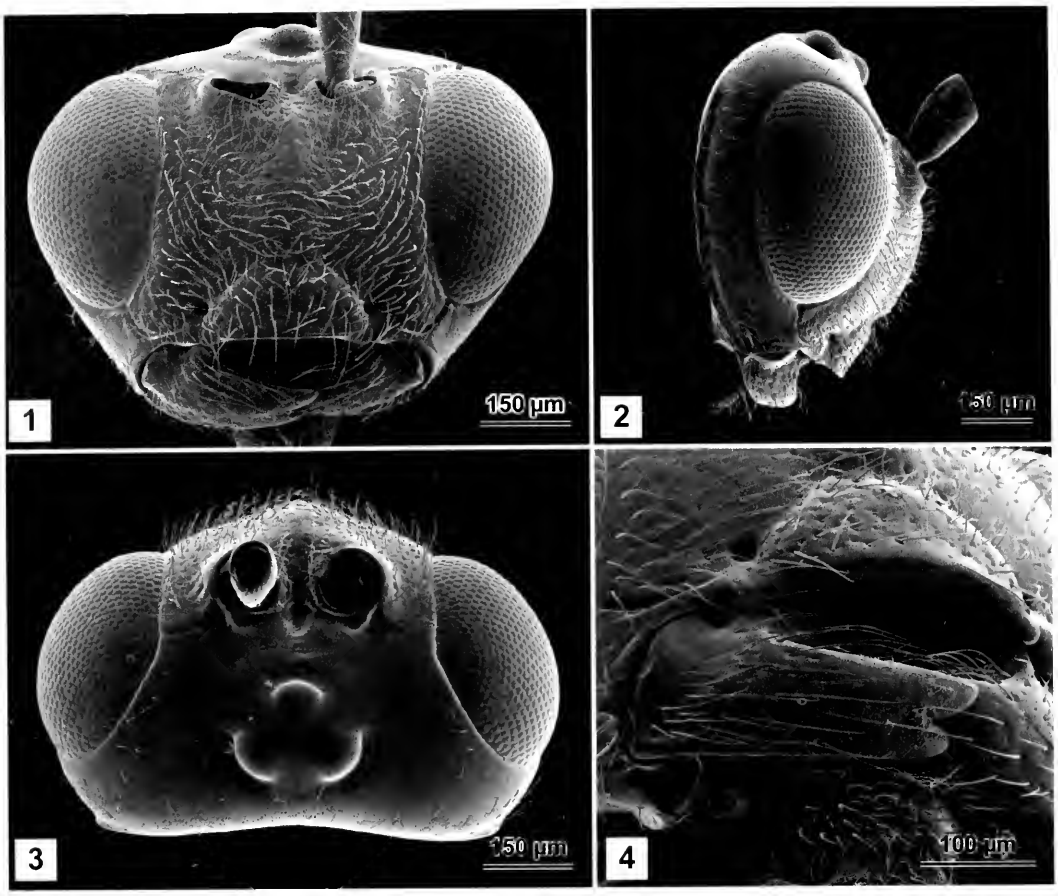
Abstract.—The opiine braconid genus *Sternaulopius* Fischer is recognized as valid, redefined, and one new species, ***Sternaulopius duplicatus***, from Madagascar, is described. The type species, *Sternaulopius bisternaulicus* Fischer, is fully redescribed, with new host and distribution records. The only other previously included species, *Sternaulopius beieri* Fischer, is placed as a junior subjective synonym of *Opius bajulus* Haliday, **new synonym**. *Opius bajulus* is also redescribed and the genus group name ***Biophthora*** Foerster is resurrected for this species. *Opius rossicus* Szépligeti, is transferred to the genus *Biophthora* (**new combination**) and *Opius castaneus* Granger, type species of *Frekius* Fischer, is transferred to *Utetes* Foerster (**new combination**). Thus, *Frekius* is a junior subjective synonym of *Utetes*, **new synonym**, but is retained as a valid subgenus. *Biophthora* and *Sternaulopius* are compared to *Xynobius* Foerster (where *Opius bajulus* has frequently been placed), and *Xynobius* is redefined and treated as a subgenus of *Eurytenes* Foerster. *Stigmatopoea* Fischer is also recognized as a valid subgenus of *Eurytenes*. Characters used to define these genus-group taxa are discussed in detail, with emphasis on venation, placement of metasomal spiracles, and sculptural details of the body. Use of the term sternaulus for a longitudinal groove on the ventral mesopleuron in Ichneumonoidea is reviewed, and it is shown that the sternaulus in cryptine and mesochorine Ichneumonidae is not homologous to the precoxal sulcus in Braconidae based on dissections of associated thoracic musculature. A true sternaulus, defined internally as the ridge supporting the origin of the mesopleural-basalare muscle, is rarely present in Braconidae.

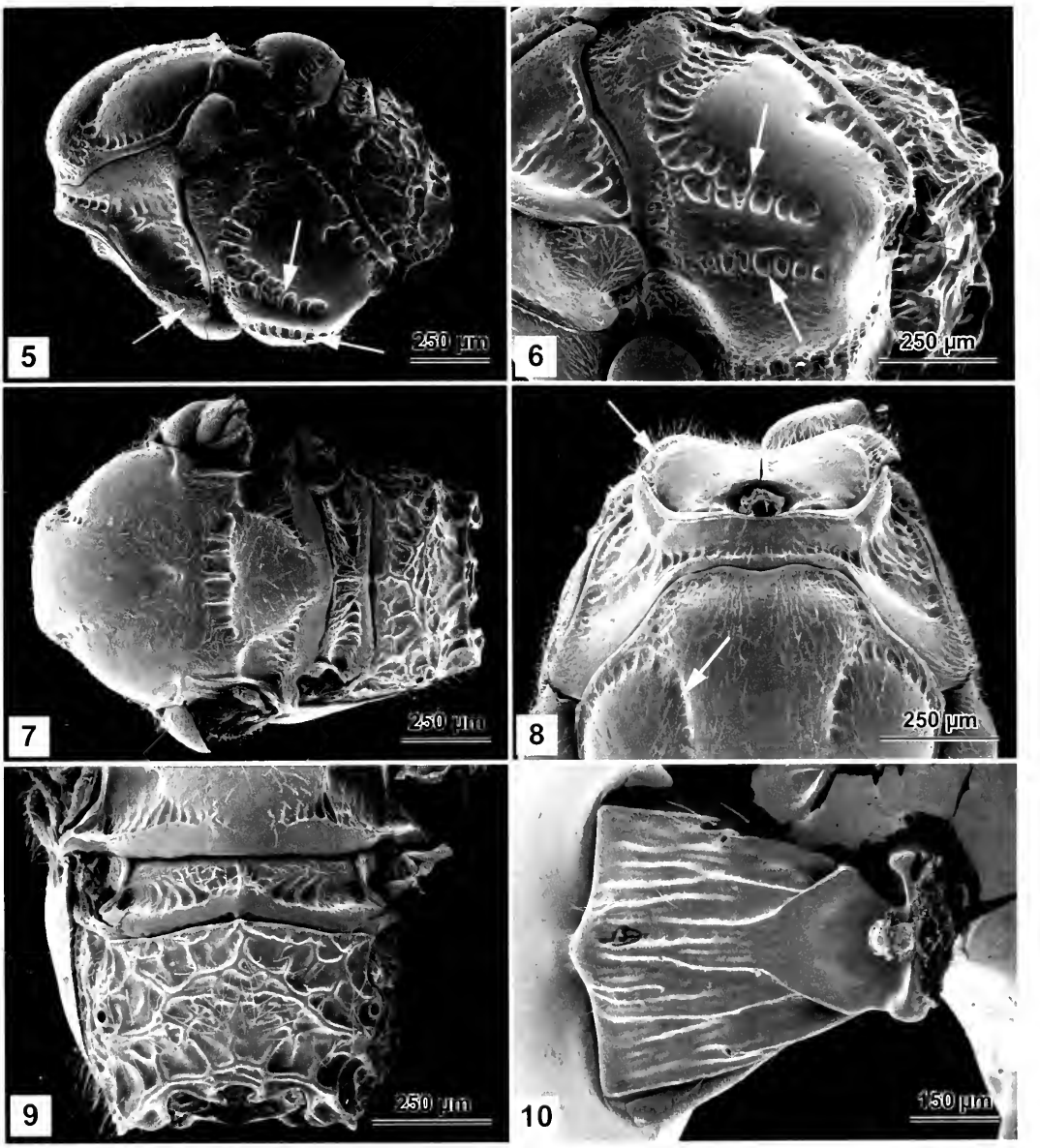
The genus *Sternaulopius* Fischer, 1965 was described to accomodate a single species from the Democratic Republic of the Congo. Subsequently, Fischer (1968) described a second species from Germany. No additional species have been described, and only five specimens have been recorded (Fischer 1965, 1972, Quicke et al. 1997). The two species that have been included in *Sternaulopius* (Figs 1–20) have two distinct grooves (sternauli) on each side of the mesopleuron but in nearly all other braconid wasps only a single groove is present, or the groove is completely lost (exceptions include *Trigastrotheca laikipiensis* Quicke and some species of *Pambolus* Haliday). These two species of *Sternaulopius* are thus distinctive, though their placement in the classification of the Opiinae is still unsettled. Wharton (1988) observed that, except for the double sternaulus, the two described species more closely resembled other species within *Opius* Wesmael *s. l.* than they did each other. On this relatively limited evidence, Wharton (1988) transferred both species to *Opius*, thus treating *Sternaulopius* as a synonym of *Opius* while at the same time noting that *Opius s. l.* was not demonstrably monophyletic. Quicke et al. (1997) recognized six genera that were formerly treated by Fischer (1972, 1977, 1987) as subgenera of *Opius*, and reported that the venom apparatus of a specimen of *Sternaulopius beieri* Fischer resembled that of some, but not all of the species that they included in one of these genera, *Xynobius* Foerster. Nothing else has been published on *Ster-*



Figs 1–4. *Sternaulopius bisternaulicus* reared from *Strombosia* fruits: 1, face. 2, lateral view of head. 3, dorsal view of head. 4, right mandible, with oblique views of clypeus and labrum.

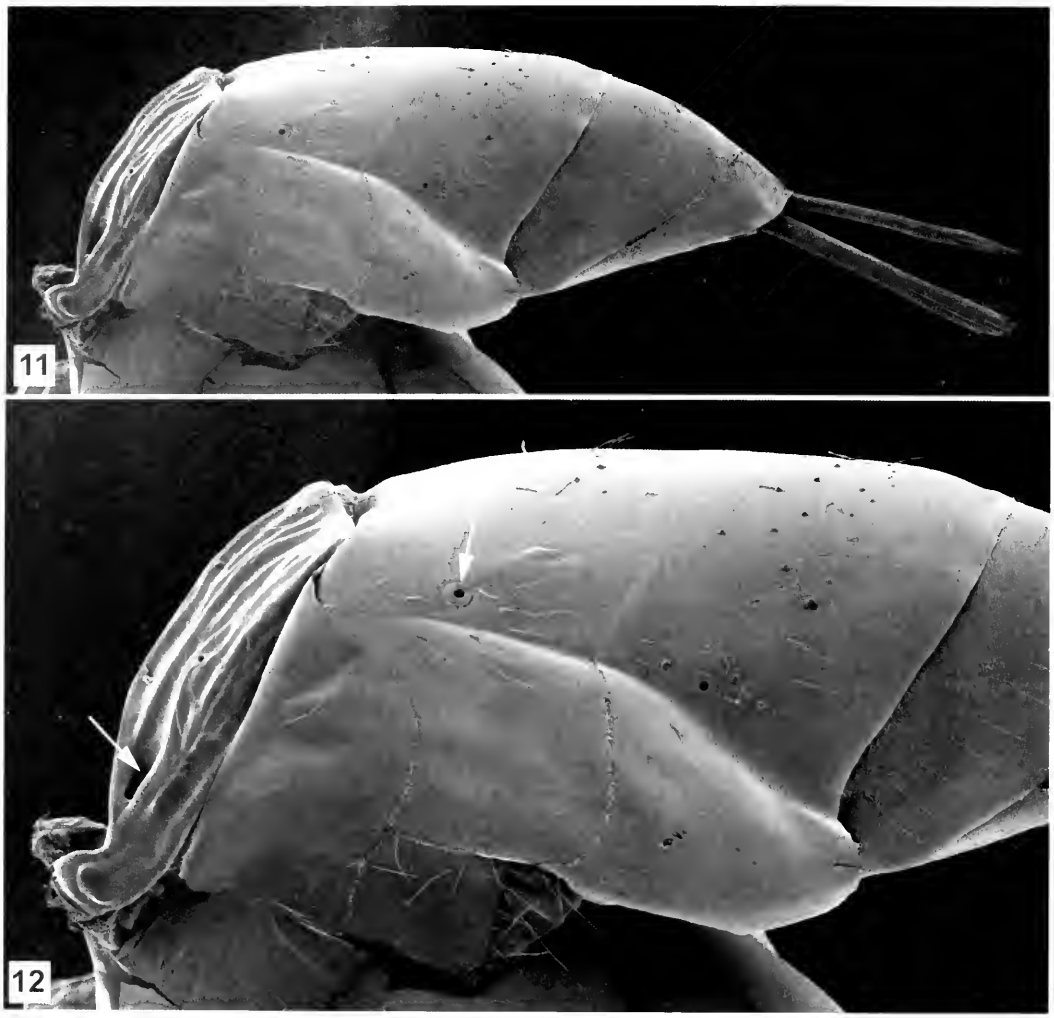
naulopius, undoubtedly due to the paucity of individuals available for study. Van Achterberg (2004) recently re-characterized *Xynobius*, but made no mention of *Sternaulopius*.

The term sternaulus has long been used by students of Ichneumonidae to describe a longitudinal groove on the lower part of the mesopleuron extending posteriorly from the ventral-lateral region of the epicnemial (= prepectal) carina towards the coxifer (or pleural coxal process) (Viereck 1916, Richards 1956, Townes 1969). Several workers (e.g. Granger 1949, Fischer 1958, Mason 1964, Marsh 1971, Wharton et al. 1997) have also applied this term to a similar groove on the mesopleuron of Braconidae, while other braconid specialists have used the name precoxal suture/sulcus (notably van Achterberg 1975, 1993, Shaw and Huddleston 1991) or simply longitudinal furrow of mesopleuron (Muesebeck 1970). The term precoxal sulcus has often been applied more widely in the Hymenoptera, though not necessary consistently (compare Richards 1956 with Bohart and Menke 1976). Gibson et al. (1998) treat the sternaulus as a synonym of the transepisternal line/sulcus (though their focus is on Chalcidoidea). Fischer (1972) noted that it was probably incorrect to equate the sternaulus with the precoxal sulcus in Braconidae, and van Achterberg



Figs 5–10. *Sternaulopius bisternaulicus* reared from *Strombosia* fruits: 5, left side of mesosoma, left arrow = propleural flange, upper right arrow = precoxal sulcus, lower right arrow = sternaulus. 6, ventral-lateral view of mesopleuron, upper arrow = precoxal sulcus, lower arrow = sternaulus. 7, dorsal view of mesosoma. 8, dorsal view of pronotum, upper arrow = oblique groove on propleuron, lower arrow = left notaulus. 9, dorsal view of metanotum and propodeum. 10, dorsal view of petiole.

(1993) illustrated the two as separate structures for braconids. In a newsletter, van Achterberg (1994) stated more specifically that the difference between the sternaulus and the precoxal sulcus can be observed in some Opiinae (undoubtedly referring to *Sternaulopius*), and Pambolinae where "the sternaulus is clearly bent downwards anteriorly and situated more ventrad."



Figs 11–12. *Sternaulopius bisternaulicus* reared from *Strombosia* fruits: 11, lateral view of metasoma. 12, same showing dorsope (left arrow) and spiracle on second tergum (right arrow).

There are no published host records for *Sternaulopius* (with the exception of information I have recently included on a website: hymenoptera.tamu.edu/parofit). However, examination of material reared from fruit in both Cameroon and Kenya (Steck et al. 1983, Copeland et al. 2002), indicates that tephritid fruit flies (Diptera) are the hosts of at least some of the species of *Sternaulopius*. This reared material forms the basis for the present treatment, including a preliminary examination of the nature of the sternaulus in Ichneumonoidea.

MATERIALS AND METHODS

Specimens of *Sternaulopius* (sensu Fischer 1972, 1987) were either reared from fruits infested with Tephritidae or borrowed from museums. Rearing methods, localities, and methods of identification of flies and plants are described in Steck et al. (1983) and Copeland et al. (2002). Material was borrowed from the Koninklijk Museum voor Midden-Afrika, Tervuren, Belgium (MRAC), Museum für Naturkunde der Humboldt-Universitaet, Berlin, Germany (ZMHB), Hungarian Natural History

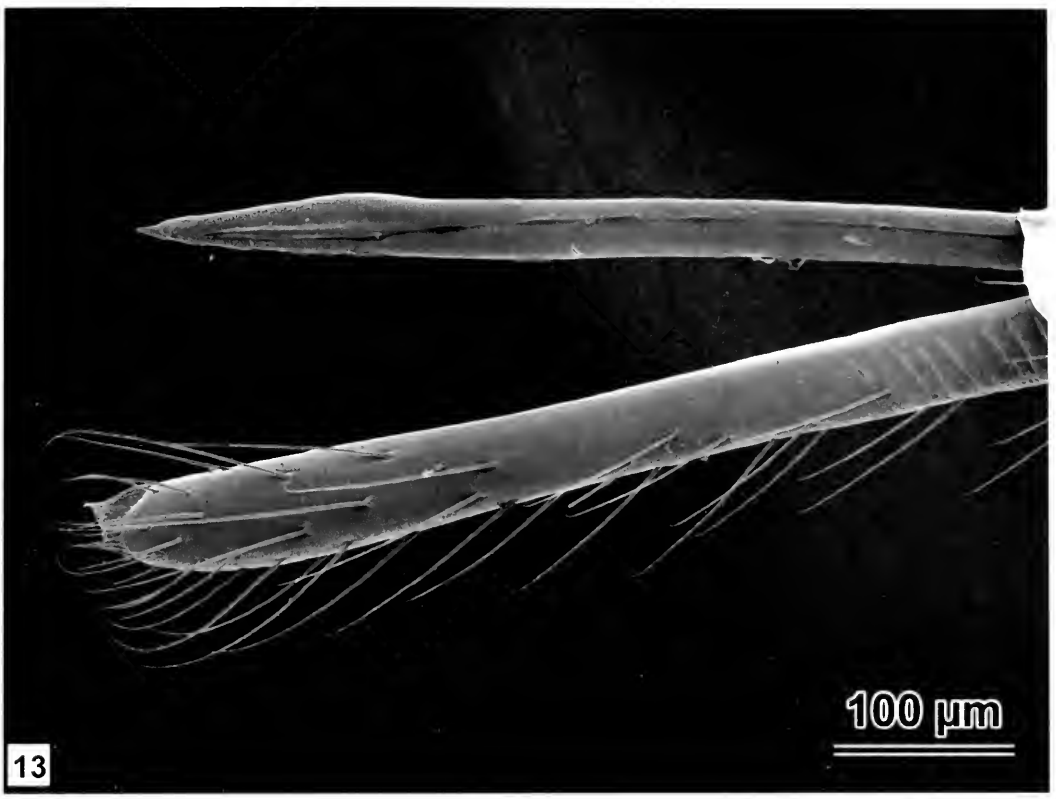


Fig. 13. *Sternaulopius bisternaulicus* reared from *Strombosia* fruits, ovipositor and ovipositor sheaths.

Museum, Budapest (HNHM), Museum National d'Histoire Naturelle, Paris (MNHN), and the U. S. National Museum of Natural History (USNM). Additional specimens examined are in the Naturhistorisches Museum Wien, Austria (NHMW) and the National Museum of Ireland, Dublin (NMID).

Fly puparia were individually isolated in Kenya by R. Copeland from one heavily-infested sample of *Strombosia scheffleri* Engl. (Olacaceae) fruit, collected in Kakamega Forest, Kenya on 30th April 2000. Association of wasps with hosts was made by the author, based on characteristics of the puparia. All other host records listed below are based on wasps that emerged from tephritid puparia that were not individually isolated.

Numerous specimens of Braconidae and Ichneumonidae from material housed at Texas A&M University were dissected to examine the internal musculature of the mesothorax. All dissected material was initially stored in 70–80% ethanol, then either air dried following transfer through 95% ethanol and 99% amyl acetate or dissected while still in alcohol. Specimens of *Apis mellifera* L. and several other Apocrita collected in central Texas with Malaise traps were also dissected to ascertain the pattern of general thoracic musculature, using the works of Daly (1964) and Gibson (1985) for orientation and identification of major muscles. All identifications were made by the author; voucher specimens are deposited as Texas A&M University voucher number 656 in the Texas A&M University Insect Collection (TAMU).

Measurements are as in Wharton (1977, 1986); terminology for descriptions of

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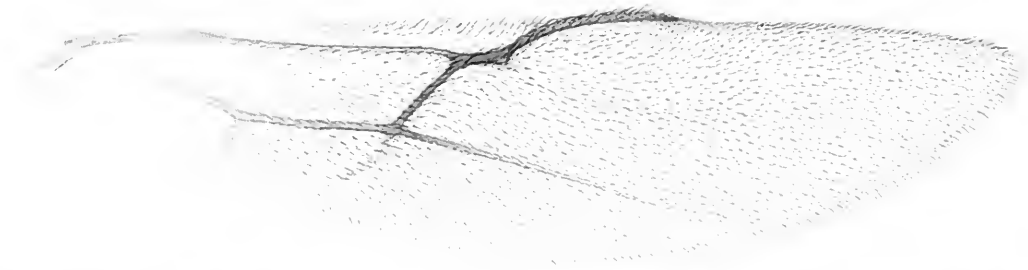

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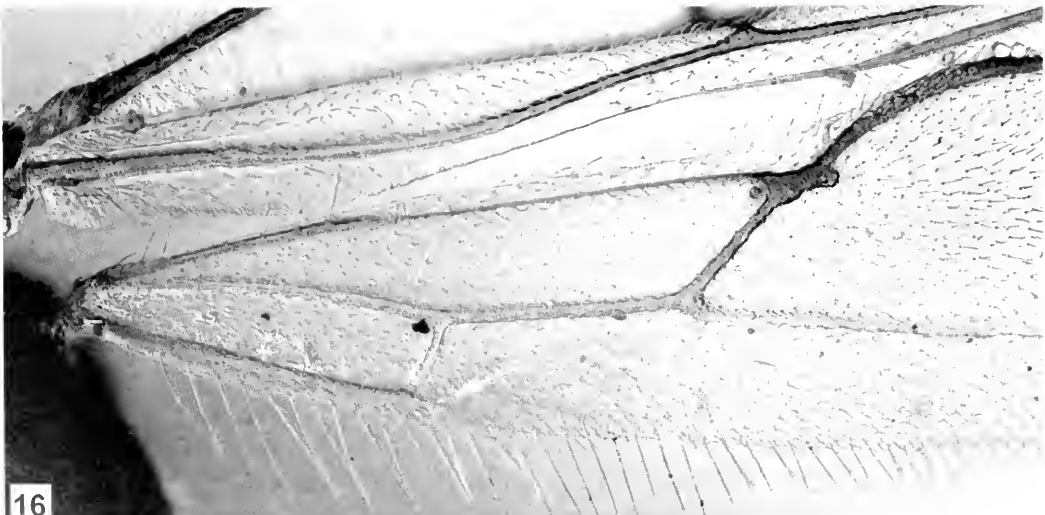


Figs 14–16. 14, 15, Fore and hind wings of *Sternaulopius bisternaulicus*. 16, Hind wing of *Biophthora bajulus*, arrow = 2-1A.

venation and external features of the body follows Sharkey and Wharton (1997), except that in the present paper a distinction is made between the sternaulus and the precoxal sulcus (following van Achterberg 1993). Details of the mesothorax associated with the musculature are provided in the results and discussion where additional

Figs 17–20. *Sternaulopius beieri* holotype female (= *B. bajulus*): 17, lateral habitus. 18, face. 19, dorsal-posterior view of posterior part of mesosoma showing mesonotal midpit and sculpture of scutellum and propodeum. 20, lateral oblique view of mesosoma, upper arrow = precoxal sulcus, lower arrow = sternaulus.

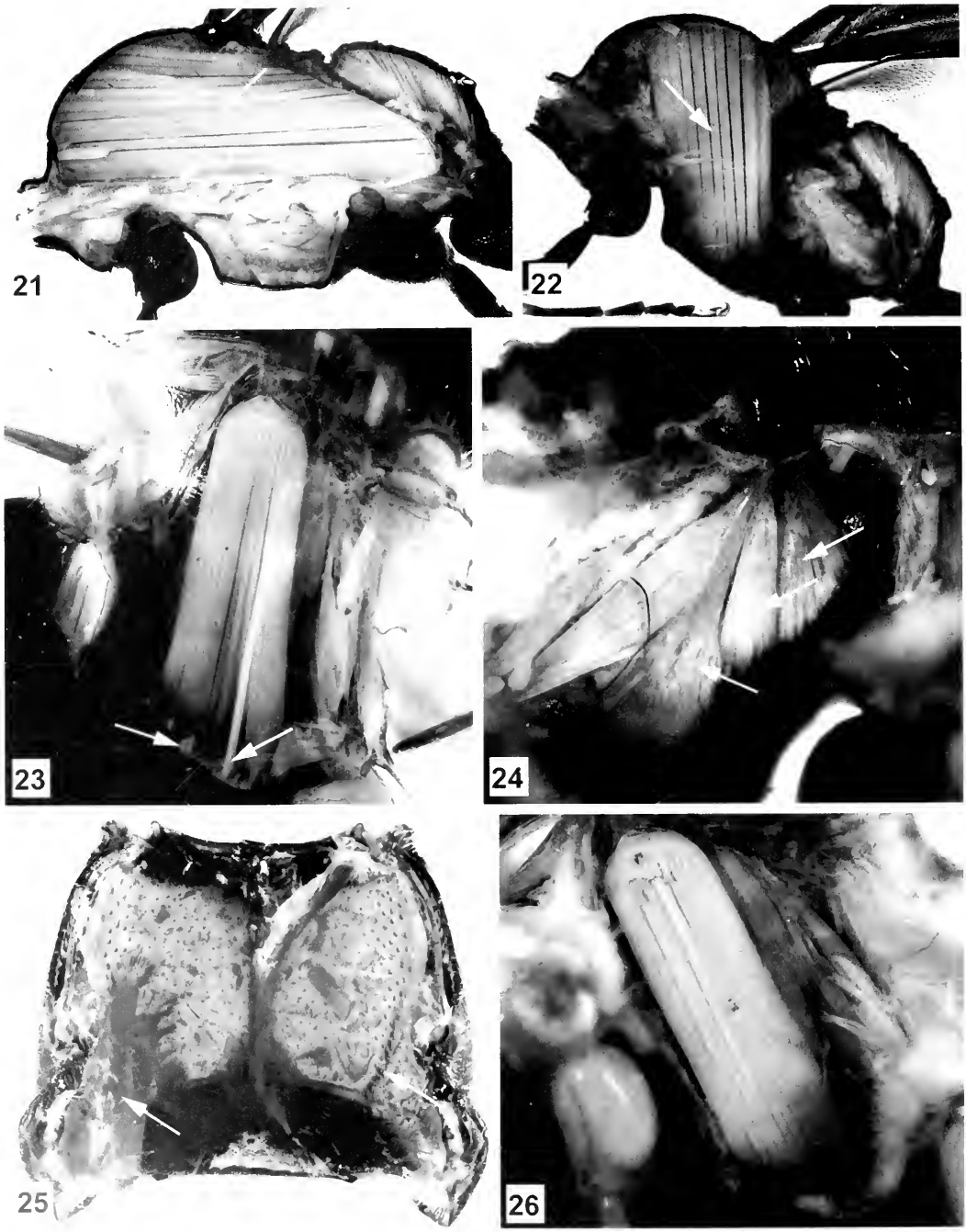
terms, when used, are specifically defined. Thoracic muscles relevant to discussions of the sternaulus are noted in Figs 21–32. Of particular focus are various axillary muscles and especially the mesopleural-basalare muscle (sensu Gibson 1985). The latter originates on the wall of the mesopleuron and inserts on the basalare sclerite near the base of the wing, at least in all the Ichneumonoidea (22 genera) and Aculeata (4 genera) examined (Table 1).

RESULTS AND DISCUSSION

Musculature and associated external features

The observations made here refer specifically to the Ichneumonoidea (Ichneumonidae + Braconidae). However, they will also apply to many other taxa both within and outside apocritan Hymenoptera, as evidenced by the detailed studies of Daly (1964) and Gibson (1985, 1986a, b, 1993). The major muscles discussed below for the Ichneumonoidea were roughly similar in their points of origin and insertion in the few aculeates and non-aculeate apocritans that were dissected (namely *A. mellifera*, *Rhopalosoma nearcticum* Brues, and undetermined species of *Gasteruption* Latreille and *Polistes* Latreille). Many of the details of thoracic musculature found in such excellent works as those of Gibson (1985, 1993) have been omitted here since the major interest is to provide a better characterization of the sternaulus.

On the mesopleuron, the sternaulus and various pits, depressions, or other changes



Figs 21–26. Sections through mesosomas of Ichneumonidae, showing thoracic musculature. 21–24, *Limonethe* sp., a typical Ichneumoninae lacking a sternaulus, left side of body in ethanol: 21, dorsolongitudinal indirect flight muscle (arrow); 22, dorsolongitudinal muscle and associated phragma removed to expose dorsoventral indirect flight muscle (arrow); 23, dorsoventral muscle removed (arrows = fragments left to show origin of this muscle mass) to expose mesopleural-basalare muscle originating in trough of mesopleuron immediately laterad dorsoventral muscle; 24, mesopleural-basalare muscle removed to expose 3 sets of muscles (arrows) originating on lateral wall of mesopleuron. 25, *Barichneumon* sp., Ichneumoninae, dorsal view of inside of trough of

in elevation are, to a greater or lesser extent, the external representation of the attachment of the thoracic muscles. Internally, the mesothorax, at least in ichneumonoids and aculeates, is dominated by the massive dorsolongitudinal (Fig. 21) and dorsoventral (Fig. 22) indirect flight muscles. The former originates largely from the median mesoscutal lobe (and partly from the phragma along the anterior margin of the lobe) and extends posteriorly through the middle of the mesothorax. On either side of this median muscle mass is a broad band of dorsoventral muscle fibers (Fig. 22), which insert on the lateral lobes of the mesoscutum and originate ventrally on the mesothorax. The floor of the mesothorax, where the dorsoventral muscles originate, is a trough interrupted medially by a phragma representing the midventral invagination of the mesosternum (partially shown in Figs 25 and 29). The lateral and ventral sides of the trough are formed on each side of the body by the relatively sharp vertical to horizontal transition in the mesepisternal wall ventrally as it curves towards the ventral midline.

Notauli are perhaps best defined as external grooves on the mesoscutum indicating the position of the internal ridge or phragma that separates the attachment point of the dorsolongitudinal muscle mass from the attachment points of the right and left dorsoventral muscle bundles (see the excellent discussion in Gibson (1985) for terminology of mesonotal grooves). In Ichneumonoidea, the position of these grooves, when present, relative to the attachment points of these two indirect flight muscles confirms that they should be called notauli (as they are in nearly all recent taxonomic treatments), rather than parapsidal furrows.

Immediately laterad the dorsoventral indirect flight muscle is the smaller (though still fairly large) mesopleural-basalare muscle (Figs 23, 25–29, 31). This is a distinctive band of muscle fibers readily identified by the dorsal, sclerotized cap that is strongly constricted to form a tendon-like attachment connected to the basalare (Figs 27, 29, 31). In Ichneumonoidea, the mesopleural-basalare originates ventrally in the trough of the mesothorax just laterad the dorsoventral muscle or it may arise somewhat higher on the vertical wall of the mesepisternum. The subtegular (= subalar) ridge, immediately ventrad the anterior subalar depression of van Achterberg (1988), is the external representation of the internal pocket in which resides the sclerotized cap of the mesopleural-basalare muscle. The epicnemial carina, when present, delineates the anterior border of this muscle mass ventrally, and dorsally it is delineated by the pronotal-mesopleural suture.

The mesopleural-basalare muscle originates on the sternaulus in those members of the Ichneumonidae that possess a sternaulus (Figs 25, 28), but does not originate on the structure that has frequently (e.g. Sharkey and Wharton 1997) been called the sternaulus in Braconidae (Figs 29–30). In the ichneumonid taxa Cryptini and Mesochorinae, both of which have a well-developed sternaulus ventrolaterally on the mesepisternum, the mesopleural-basalare muscle originates on the internal ledge formed by the anterior portion of the sternaulus as the latter extends posteriorly from the epicnemial carina. In those mem-

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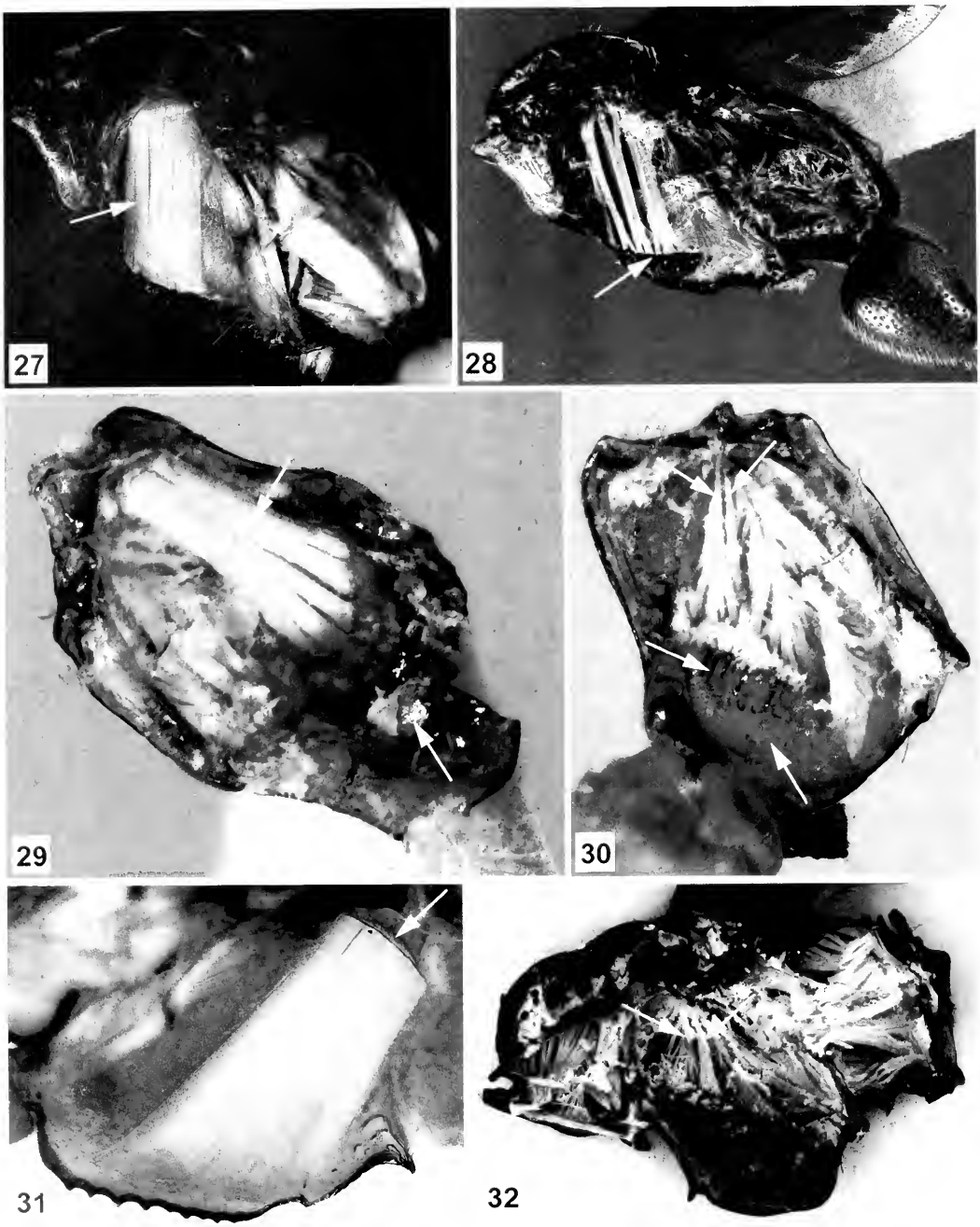
mesopleuron, dried specimen, left arrow showing mesopleural-basalare muscle, right arrow showing internal ledge of short sternaulus on which anterior end of mesopleural-basalare originates. 26, *Enicospilus* sp., Ophioninae, right side of body in ethanol, showing origin of elongate mesopleural-basalare in trough of mesopleuron.



Figs. 27–32. Longitudinal sections through mesosomas of Ichneumonoidea, showing muscles originating on mesopleuron: 27–28, Ichneumonidae, Cryptinae, right side of body: 27, in ethanol showing mesopleural-basalare muscle (arrow) and its dorsal cap; 28, same specimen, dried (resulting in gaps in muscle bundle), showing origin of mesopleural-basalare muscle on internal ledge formed by sternaulus (arrow). 29–30, *Fopius vandenboschi* (Braconidae, Opiinae), dried: 29, ventral and left portions of body, bottom arrow = midventral phragma (partially broken in dissection), top arrow = mesopleural-basalare muscle; 30, right side of body, mesopleural-basalare removed, bottom arrow = region where mesopleural-basalare originates, middle arrow = precoxal sulcus visible through cuticle, top two arrows = muscles inserting on axillary sclerites. 31, *Wroughtonia ferruginea*

bers of the subfamily Ichneumoninae in which the sternaulus is distinct as a short anterior crease (e.g. Fig. 25), the mesopleural-basalare also originates there, providing evidence that the sternaulus in these three subfamilies is homologous. In the pimplines, ichneumonines, and campoplegines that lack a visible sternaulus, the mesopleural-basalare muscle originates at the lateral margin of the ventral curve of the mesepisternum just laterad the origin of the dorsoventral indirect flight muscle (Figs 21–23, 26). This is also where the mesopleural-basalare originates in all of the braconids that were dissected. The sternaulus is long in nearly all cryptines and tends to curve dorsally as it extends posteriorly. However, in the species dissected, the mesopleural-basalare is attached to the anterior end of the sternaulus, which is more ventrally displaced. In those braconids with a well-developed "sternaulus," such as members of the Agathidinae, Doryctinae, Helconinae, and Rogadinae, the mesopleural-basalare passes over this "sternaulus" from its more ventral origin on the floor of the mesopleuron. In both braconids and ichneumonids, the muscle varies in length and width (compare Fig. 29 with Fig. 31), as might be expected given the differences among species in the shape of the mesothorax.

In the opiine braconid *Sternaulopius*, which has a second "sternaulus" below the first, the mesopleural-basalare muscle originates on the internal ledge formed by the ventral-most sternaulus, which, not coincidentally, is in the same position as the attachment point of this muscle in other braconids. The dorsal-most "sternaulus" in *Sternaulopius* is homologous to the "sternaulus" of other braconids, and on the inside, the ledge along the dorsal side of this braconid "sternaulus" serves as a general attachment point for three sets of muscles located laterad the mesopleural-basalare muscle (the ledge best seen in Fig. 30 where this "sternaulus" is visible through the semi-transparent cuticle). All three of these muscles are fan-shaped, with a broad origin on the wall of the mesopleuron. They are strongly tapered dorsally, where the muscle bundles in each fan unite to form tendons (Figs 24, 30, 32). Two of these muscles appear to correspond to the muscles numbered 8 and 9 in Gibson (1986b) and are clearly axillary muscles, inserting on the third axillary sclerite at the base of the fore wing. The third is similar in position to Gibson's (1986b) muscle number 4, and inserts on the mesoscutum near the posterior notal wing process. This same pattern of three muscles was found in all ichneumonoids examined. However, the position of the muscles and in particular their orientation (nearly longitudinal vs. dorsoventral) varies with the shape of thorax and, in braconids, the angle of the "sternaulus." When the braconid "sternaulus" is strongly oblique, for example, the dorsal-most of the axillary muscles may be nearly longitudinal rather than dorsoventral in orientation.

Although the origin of a muscle may be less stable than the insertion for establishing homologies (see especially Daly 1963, 1964), the above observations support the conclusions of van Achterberg (1993, 1994) that the ventral sternaulus in *Sternaulopius* is homologous to the sternaulus of ichneumonids. Similarly, the dorsal "sternaulus" of *Sternaulopius* is homologous to the single groove found in other braconids, which van Achterberg has termed the precoxal

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(Braconidae, Helconinae), left side of body in ethanol, showing broad mesopleural-basalare muscle, arrow = dorsal cap of muscle. 32, *Alabagrus* sp. (Braconidae, Agathidinae), right side of body, dried, mesopleural-basalare muscle removed, arrows = muscles inserted on axillary sclerite.

Table 1. List of taxa dissected for examination of mesopleural-basalare and other mesothoracic muscles.

BRACONIDAE
Agathidinae
Alabagrus sp., College Station, TX, USA
Braconinae
Atanycolus simplex (Cresson) and *Digonogastra* sp., College Station, TX, USA
Cenocoeliinae
Cenocoelius saperdae (Ashmead), College Station, TX, USA
Doryctinae
Heterospilus sp., Gainesville, FL, USA
Helconinae
Helconidea ferruginea (Brues), College Station & Angelina National Forest, TX, USA
Homolobinae
Homolobus truncator (Say), Conroe, TX, USA
Macrocentrinae
Austrozele sp., Gainesville, FL, USA
Opiinae
Fopius arisanus (Sonan), Honolulu, HI, USA
Fopius vandenboschi (Fullaway), Tangerang, W. Java, Indonesia
Psyttalia incisi (Silvestri), Honolulu, HI, USA
Sternaulopius bisternaulicus Fischer, coastal Kenya
Rogadinae
Aleiodes aciculatus Cresson, College Station, TX, USA
ICHNEUMONIDAE
Anomaloninae
Anomalon sp., Conroe, TX, USA
Banchinae
Syzeuctus sp., Conroe, TX, USA
Cryptinae
Cryptini spp., College Station, TX, USA and Springfield, Dominica
Ichneumoninae
Barichneumon sp., Bastrop, TX, USA
Cratichneumon sp., Huntsville, TX, USA
Limonethe sp., Gainesville, FL, USA
Mesochorinae
Mesochorus sp., College Station, TX, USA
Ophioninae
Enicospilus sp., Gainesville, FL, USA
Pimplinae
Pimpla sp., College Station, TX, USA
Rhyssinae
Megarhyssa macrurus (L.), College Station, TX, USA
APIDAE
Apis mellifera L., College Station, TX, USA
GASTERUPTIIDAE
Gasteruption sp. (*Rhydinofoenus* sensu Townes), College Station, TX, USA
RHOPALOSOMATIDAE
Rhopalosoma nearcticum Brues, College Station, TX, USA
VESPIDAE
Polistes sp., College Station, TX, USA

sulcus. The sternaulus of ichneumonids has the same function as the "sternaulus" (= precoxal sulcus) of most braconids, but the muscles whose origin they support are different and thus the structures are unlikely to be homologous. It therefore seems appropriate to use the term precoxal sulcus for the more dorsally displaced groove found in most braconids, despite the probability that this term is used for non-

homologus features in other Apocrita. Coining another term would simply add to the confusion, and seems unnecessary since precoxal sulcus has become fairly well established at least in the European braconid literature.

Taxonomy

Sternaulopius Fischer, 1965

Sternaulopius Fischer, 1965: 311.

Type species: *Sternaulopius bisternaulicus* Fischer, 1965. Monobasic and original designation.

Head (Figs 1–4). Occipital carina widely separated from hypostomal carina at base of mandible, extending dorsally more than half height of head, not or only weakly curved medially at dorsal end, completely absent dorsal-medially; hypostomal carina protruding as a flange below base of mandible. Gena (including temple behind eye) and vertex smooth, polished. Frons bare, polished and impunctate but usually with weak, irregular sculpture along midline. Mandible (Fig. 4) evenly curved along dorsal margin; ventral margin distinctly carinate, without basal tooth or lobe; bidentate, dorsal tooth longer than ventral tooth; outer surface of mandible weakly to stongly curved from base to apex, species with weaker curvature have a completely concealed labrum. Labrum varying from exposed to completely concealed; clypeus (Figs 1, 2, 4) with ventral margin truncate, varying from sharp (when labrum exposed) to slightly thicker (when labrum concealed), in profile clypeus evenly convex, moderately protruding, distinctly overhanging labrum when the latter exposed. Epistomal sulcus generally more deeply impressed laterally than dorsally. Malar sulcus a distinctly impressed line. Maxillary palp about as long as height of head, 6 segmented; labial palp 4 segmented. First flagellomere longer than second; apical flagellomere spinose at tip.

Mesosoma (Figs 5–9). Propleural flange large, strongly curved laterally to partially conceal ventral corner of pronotum above base of fore coxa; oblique carina and associated, shallow groove (Fig. 8) weakly to distinctly developed, separating flange from rest of propleuron. Pronotum dorsally with transverse, crenulate groove along posterior margin; pronope absent. Notauli deep anteriorly, shallow to barely indicated posteriorly, weakly curving into distinct, rounded midpit; unsculptured posteriorly. Mesoscutum carinately margined laterally from base of notaulus to axillary flange (Fig. 5). Transscutal articulation represented by a distinct sulcus immediately anteriorad crenulate scutoscutellar sulcus. Scutellum (Fig. 7) polished, unsculptured to weakly punctate (except along posterior margin). Precoxal sulcus (Fig. 6) broad, crenulate anteriorly, absent or apparently so posteriorly; distinct from the more ventrally placed sternaulus; sternaulus well-developed as a broad, crenulate groove extending more than half length of mesopleuron; both precoxal sulcus and sternaulus straight over posterior half, never curving ventromedially. Hind margin of mesopleuron crenulate above (though sometimes weakly) and below mesopleural fovea (Figs 5, 6). Ventral midline crenulate, with carinations distinct posteriorly but not developed as a postpectal carina. Metapleural/propodeal junction either obscured by sculpture or represented by a weak impression. Propodeum rugose to carinate-rugose. Hind tibia lacking basal carina typical of *Utetes* Foerster, 1862.

Wings (Figs 14, 15). Stigma thickened, wedge-shaped; r arising from basal 0.3–0.4; second submarginal cell long (2RS<3RSa); m-cu arising distad base of 2RS, (RS+M)b thus absent; (RS+M)a arising distinctly below parastigma, 1RS>0.3×1M; 1-1A curved towards posterior margin but remaining separate from margin by at least width of 1-1A; 1st subdiscal cell closed. Hind wing RS nearly absent, represented by a weak, unpigmented crease; m-cu extending at least half distance to wing

margin as a curved, distinctly impressed, weakly pigmented line.

Metasoma (Figs 10–12). Petiole with spiracle located near middle of segment; pit-like dorsope present basally at junction of dorsal and lateral carinae; laterope present at extreme base. Second and following visible terga neither sculptured nor unusually shortened. Second metasomal tergite with spiracle placed dorsally, just mesad the rounded lateral fold. Hypopygium weakly protruding at midline, never strongly attenuate nor extending beyond metasomal tergites. Ovipositor lacking sharp subapical notch.

Biology.—Reared from tephritids infesting fruits belonging to several plant families. Known only from Subsaharan Africa and Madagascar. Included species: *Sternaulopius bisternaulicus* Fischer, 1965 and the new species from Madagascar described below.

Excluded species.—*Sternaulopius beieri* Fischer, 1968 (= *Opius bajulus* Haliday, 1837).

Diagnosis.—*Sternaulopius* is distinguished from nearly all other supraspecific taxa in the Opiinae by the presence of both a sculptured precoxal sulcus and a true sternaulus (Fig. 6), and from *Biophthora* by the absence of rugose sculpture on the scutellum dorsomedially. *Sternaulopius* is further recognizable by the presence of a dorsope, a distinct median pit on the mesoscutum, and a five-sided second submarginal cell, as well as the absence of both a basal tooth or lobe on the mandible and a basal carina on the hind tibia.

Remarks.—The type species of *Sternaulopius* was described on the basis of one female and two males from the Democratic Republic of the Congo (Fischer 1965). A second species, *Sternaulopius beieri* Fischer, was subsequently described from Germany on the basis of a single female (Fischer 1968). Only one additional specimen has been reported to date (Quicke et al. 1997). The discovery that *S. beieri* is a junior synonym of *Opius bajulus* Haliday, 1837 (**new synonym**, see below) affords an opportunity to compare *Sternaulopius* to *Xynobius* Foerster, 1862 as well as to discuss the placement of *Sternaulopius* within the Opiinae.

Although *O. bajulus* has been placed in *Xynobius* in all recent treatments of Opiinae (e. g. Fischer 1972, Tobias and Jakamavicius 1986, van Achterberg 1997, 2004; Quicke et al. 1997), there are distinct differences between *bajulus* and the type species of *Xynobius* (*viz*, *X. pallipes* Foerster, 1862, for which the current valid name is *Eurytenes caelatus* (Haliday, 1837), **new combination**, see below). One of the more important of these differences is the arrangement of metasomal spiracles. In *E. caelatus* (as well as in *Eurytenes abnormis* (Wesmael, 1835), the type species of *Eurytenes* Foerster, 1862), the spiracle of the second metasomal tergum is situated laterally, well below the crease that separates the dorsal portion of the tergite from the lateral portion of the tergite. In both *bisternaulicus* and *beieri* (=*bajulus*), the spiracle (Fig. 12) is located dorsally in a position typical of most other opiines: either adjacent to the crease (when a distinct crease is present) or situated more medially. *Xynobius* was originally described as a cyclostome braconid (Foerster 1862), but Foerster obviously had difficulty placing this taxon since in the same paper he described two other genera (*Biophthora* Foerster, 1862 and *Aclisis* Foerster, 1862) in two different family-group taxa that are now (Fischer 1972, van Achterberg 2004) included in *Xynobius*. Muesebeck and Walkley (1951) were apparently the first to associate the name *Xynobius* with Opiinae when they placed all three of these Foerster genera as synonyms of *Opius* Wesmael, 1835. Fischer (1972) established a comprehensive classification for the Opiinae that included *Xynobius* as one of 36 subgenera of *Opius*. Fischer (1972) presented the first clear delineation of *Xynobius*, which he characterized based on its exposed labrum and sculptural

features of the mesothorax. He noted especially the heavily sculptured scutellum (Fig. 19), an unusual feature in the Opiinae, and this is shared by both *bajulus* and *caelatus*. Both species have been characterized as having an exposed labrum and also a deep, pit-like dorsope on the petiole, features emphasized by Tobias (1977) and van Achterberg (2004) respectively. Thus, both of these species have been included in *Xynobius* since 1972 regardless of the differences in how *Xynobius* has been characterized by Fischer (1972) and subsequent authors, and regardless of whether *Xynobius* has been accorded subgeneric (Fischer 1972, Tobias 1977) or generic (van Achterberg 1997, 2004) rank. Thus, if *bajulus* is retained in *Sternaulopius*, following the discovery here of the synonymy between *bajulus* and *beieri*, then *Sternaulopius* becomes a synonym of either *Xynobius* or *Biophthora* (*bajulus* is the type species of *Biophthora*).

The difference between *bajulus* and *caelatus* in placement of the spiracle of the second metasomal tergum argues against retention of *bajulus* in *Xynobius*. Differences in the details of fore wing venation and shape of the clypeus, mandibles, and petiole provide further evidence that *bajulus* and *caelatus* may not be closely related, and bring into question the homology of some of the character states previously used to place these two species together in *Xynobius*. The second submarginal cell is parallel-sided in *caelatus*, m-cu is antefurcal, the stigma is more nearly parallel-sided than wedge-shaped, the clypeus is short and strongly protruding, the mandible is more massive basally and strongly tapered distally, and the dorsal carinae of the petiole are strongly convergent basally. In *bajulus* (Figs 16–20), the second submarginal cell is narrowed distally, m-cu is postfurcal, the clypeus is truncate and nearly flat (and the labrum consequently more weakly exposed), the mandible is slenderer and nearly parallel-sided, and the dorsal carinae of the petiole are widely separated throughout. Despite these differences, removal of *bajulus* from *Xynobius* is complicated by the fact that both *bajulus* and *caelatus* can be characterized by the shared possession of strongly elevated and heavily sculptured scutellum (Fischer 1972), an unusual feature found in relatively few Opiinae. In one of the other species with a similarly sculptured scutellum, *Opius severini* Fischer, 1964, the scutellum, fore wing venation, clypeus and mandible are as in *caelatus*, but the spiracle of the second metasomal segment is positioned as in *bajulus*. One is therefore left with the choice of a very broad definition for *Xynobius*, such as that offered by Tobias (1977), Tobias and Jakimavicius (1986) and, apparently, van Achterberg (2004), which could accomodate *bajulus*, or a much more restricted one (e.g. Fischer 1972). The relative merits of each are outlined below.

Throughout much of the 1900s, most Opiinae were placed in the genus *Opius*, which eventually encompassed over 1000 species. Fischer (1972) facilitated work on the Opiinae by presenting a classification in which several distinctive genera were recognized and an extensive subgeneric classification was proposed for *Opius*. *Opius* has been subsequently reduced by removal of putatively monophyletic taxa such as *Utetes* and *Psyttalia* Walker, 1860 (Wharton 1987, 1988), and by an attempt to restrict the definition of *Opius* to species with a basal tooth on the mandible (van Achterberg and Salvo 1997). Further delimitation of monophyletic groups is essential for progress in understanding the relationships and evolutionary biology of this large and important group of dipteran endoparasitoids. *Xynobius* in the sense used by Tobias (1977) and van Achterberg (2004) is fairly well delineated, but difficult to define as monophyletic because all of the characters given for recognition of the genus can be considered plesiomorphic. As correctly noted by van Achterberg (2004), for example, *Xynobius* has a number

of features suggestive of a basal placement within the Opiinae. Features such as a distinct dorsope, distinct hypoclypeal depression (labrum exposed by a gap between the clypeus and mandibles), absence of a transverse carina on the propleuron and absence of a true sternaulus may be useful for recognition of *Xynobius* within the Opiinae (van Achterberg 2004), but they are also indicative of the basal placement of this group since these features also characterize the Exothecini, the putative outgroup taxon and are thus plesiomorphic in this context. Some exothecines also have a short (relative to 2RS) cross-vein r in the fore wing, the only other recognition feature noted by van Achterberg (2004). The latter is significant because it serves to separate *Xynobius* sensu van Achterberg (2004) from *Eurytenes*.

The sculptural patterns noted by Fischer (1972) in his more restricted definition of *Xynobius* provide a seemingly better opportunity for defining this taxon as monophyletic, but there are problems of homology. The species included in *Xynobius* by Fischer all have a sculptured scutellum, but the pattern differs markedly among the species. For example, *Opius rudis* Wesmael, 1835, included in *Xynobius* by Fischer (1972), has a flattened scutellum with coriaceous sculpture lacking rugosities. In species such as *caelatus*, *bajulus*, and *severini*, the scutellum is both elevated and rugose, providing a putative synapomorph in terms of a complex character. However, this same complex character state is found in some of the species of *Biosteres* Foerster, 1862. Further, as detailed above, these three species (*caelatus*, *bajulus*, and *severini*) differ markedly in wing venation, shape of the clypeus and mandibles, and placement of the metasomal spiracles. The available evidence suggests, then, that this scutellar feature has either developed independently in at least a few opiine lineages or is a primitive feature retained in these lineages. As I am unable to provide a strong argument for the monophyly of *Xynobius* using characters emphasized by previous workers, I prefer to retain *Xynobius* as a subgenus at this time rather than elevate it to generic rank. If *Opius* is defined in a restricted sense to include only species with a basal tooth on the mandible (van Achterberg and Salvo 1997), then *Xynobius* is better placed in *Eurytenes*.

Placement of *Xynobius* in *Eurytenes* by no means solves the problem of monophyly of *Xynobius*, but does bring together several groups of opiines that share characters suggestive of a close relationship (though it is admittedly tricky to define relationships among those putatively basal taxa that retain both a deep dorsope and an exposed labrum). *Eurytenes* has long been characterized by the extremely basal origin of r on the stigma, and only two species have been described with this characteristic. As pointed out by Wharton (1988), however, the shape of the pterostigma is also unusual, and the shape of both the stigma and the petiole suggest a relationship between the type species of *Eurytenes*, *E. abnormis*, and species such as *Opius macrocerus* Thomson, 1895 (type species of *Stigmatopoea* Fischer, 1986). Critical examination of the fore wing of *macrocerus* demonstrates that the *Eurytenes* condition has been achieved by increasing the angle between r and 3RSa and increasing the length and curvature of r so that the latter extends to the base of the stigma. The close relationship between *macrocerus* and *abnormis* is further supported by other shared features of the fore wing (shape of second submarginal cell and placement of m-cu and 2CUb) as well as the fact that both have the spiracle of the second metasomal segment displaced laterally. Fischer (1998) accepted the relationship between *macrocerus* and *Eurytenes* based on fore wing venation, and in particular the shape of the stigma, and tranferred several additional species to *Eurytenes*. Van Achterberg (2004), on the other hand, placed *Stigmatopoea* as a synonym of *Xynobius*, but did not

include or discuss *Eurytenes* despite the fact that Quicke et al. (1997) included *Eurytenes* as a subgenus of *Xynobius*, citing van Achterberg and van Zuijlen (in press). In either case, *macrocerus* is nicely positioned as morphologically intermediate between *caelatus* and *abnormis*, with sufficient similarities in the shape of the stigma, the fore wing venation, and the placement of T2 spiracles to justify their grouping as a single genus. Considering only these three taxa, the hypothesized relationships are *Xynobius* + (*Stigmatopoea* + *Eurytenes s. s.*). If the shape of the elongate distal portion of the stigma is used to support the monophyly of *Eurytenes s. l.*, then the narrowed basal portion in conjunction with a relatively long vein r can be used to support a *Stigmatopoea* + *Eurytenes s. s.* relationship. However, this would be an oversimplified picture of relationships since *Eurytenes*, as defined here, embodies a fair number of species, including most of Fischer's (1998) *Eurytenes* and van Achterberg's (2004) *Xynobius*. Here, I propose restricting the name *Xynobius* to those species with the spiracle of the second metasomal segment located more laterally, though this will need to be re-evaluated in a more comprehensive treatment of this group. Therefore, I reject the inclusion of *bajulus* in *Xynobius*, though an argument could be made that *bajulus* is simply a highly derived species of *Xynobius*. Additional differences in the stigma, venation, clypeus, and mandibles all suggest that *bajulus* should be excluded not only from *Xynobius* but also from *Eurytenes s. l.* Similarly, *rudis* is also excluded from both *Eurytenes* and *Xynobius* since it lacks both the ventrally displaced T2 spiracle and a dorsope.

Rank is subjective, and thus an argument could be made for retaining both *Eurytenes* and *Xynobius* as separate genera. The shared placement of the spiracle laterally on the second metasomal segment, which differs from that in Exothecini, provides an argument against this course of action and for monophyly of the included species. Additionally, based on the above hypothesized relationships, recognition of *Eurytenes* separate from *Xynobius* would render the latter paraphyletic if *Stigmatopoea* is treated as a synonym of *Xynobius* (as in van Achterberg 2004). *Eurytenes* and *Xynobius* also compete for priority since both were described in the same publication (Foerster 1862). *Eurytenes* has been consistently recognized as a genus since it's initial description; hence my preference for use of this name over *Xynobius*. This still leaves unresolved the question of the most appropriate genus group name(s) for *bajulus* and *bisternaulicus*.

If *Opius* is temporarily maintained as a paraphyletic assemblage from which monophyletic groups are extracted as they become recognized and delineated over time, following Wharton (1988), then both *bajulus* and *bisternaulicus* can be retained in *Opius* until their relationships are better understood. A restricted definition for *Opius* is ultimately desirable, however, and since van Achterberg and Salvo (1997) have provided one, this leaves *bajulus* and *bisternaulicus* excluded from *Opius*, but with *Biophthora* and *Sternaulopius*, respectively, as available genus-group names. *Aulonotus* Ashmead, 1900 is also available for species with the second metasomal spiracle placed dorsally and possessing a distinct dorsope, a sculptured precoxal sulcus, and a mesonotal midpit. Fischer (1972) and Fischer and Koponen (1999) treated *Aulonotus* as a subgenus of *Opius*, Fischer (1998) elevated it to generic rank, and van Achterberg (2004) listed it as a synonym of *Xynobius*. *Aulonotus* is a convenient place to put species formerly placed in either *Xynobius* or *Eurytenes*, but which do not fit the restricted definition presented above. Unfortunately, the name *Biophthora*, which has remained in obscurity since originally proposed by Foerster (1862) and has been treated as a synonym since the works of Marshall (1891) and Dalla Torre (1898), has priority over the

more widely used name *Aulonotus*. *Apodesmia* and *Utetes* also date from Foerster (1862), and also have been recently treated as genera, but their definitions would have to be expanded considerably to accomodate *bajulus* and/or *bisternaulicus* since the type species of both *Apodesmia* and *Utetes* lack a dorsope. *Biophthora* Foerster, **new status**, is thus the most suitable genus group name for *bajulus* and *Sternaulopius* is the most suitable name for *bisternaulicus*.

Following the discovery of a species from Madagascar (described below) with clypeus and mandibles resembling *bajulus* but otherwise more closely resembling *bisternaulicus*, it has become much more challenging to find morphological differences useful for retaining *Sternaulopius* and *Biophthora* as separate genera. In addition to similar sculptural features already noted, the venation of fore and hind wing is nearly identical (and similar to many other opiines). Nevertheless, I retain them as separate largely because *Sternaulopius* is an Afrotropical group of tephritid parasitoids and *bajulus* is a temperate species with the general habitus and short ovipositor suggestive of it being a leaf-miner parasitoid. In addition to differences in the ovipositor and shape of the metasoma, *bajulus* has a rugose, elevated scutellum. Other, seemingly more trivial, differences are noted in the descriptions below.

Sternaulopius bisternaulicus Fischer, 1965

(Figs 1–15)

Sternaulopius bisternaulicus Fischer, 1965: 312–314, holotype female in MRAC; Fischer 1968: 105, key. Fischer 1971a: 125, catalog; Fischer 1987: 562–564, redescription, figures; van Achterberg 1993: 121, figures; Yu and van Achterberg 2005, electronic catalog.

Opius bisternaulicus: Wharton 1988: 355–357.

Redescription.—Head (Figs 1–4) in dorsal view 1.8–2.0 × broader than long, 1.40–1.55 × broader than length in lateral view, eyes distinctly bulging, width at eyes 1.05–1.10 × width at temples; face 1.45–1.65 × wider than high; eye in lateral view large, 2.9–3.9 × longer than temple. Frons, vertex, and occiput highly polished, face appearing less polished due to punctation; low, median ridge present from epistomal sulcus to level of antennal bases, replaced on frons by shallow, median, crenulate line extending to or nearly to median ocellus; area between and immediately posteriorad antenna often weakly rugulose; face distinctly punctate throughout, punctures separated by about their own diameter; frons with 3–5 setae near eye margin, vertex and frons otherwise bare; occipital margin with a single row of setae dorsally. Width of ocellar field 1.1–1.5 × distance from lateral ocellus to eye; width of ocellar field 2.2–2.8 × width of lateral ocellus. Hypostomal carina protruding as a short but distinct flange beneath mandible when mandible closed; occipital carina widely separated from hypostomal carina ventrally (separation about equal to basal width of mandible), sharp and distinctly elevated throughout, extending dorsally just below top of eye in lateral view, not reflected medially at dorsal terminus; very shallowly curved in lateral view. Malar space distinct, 0.15–0.25 × eye height, a little shorter than basal width of mandible; punctate (similar to face) between distinct malar sulcus and margin of clypeus, smooth and polished laterad sulcus. Clypeus about twice wider than high; truncate ventrally in frontal view, slightly protruding ventrally in profile; nearly triangular in outline, the epistomal sulcus only weakly curved; uniformly punctate, pattern of punctation as on face; epistomal sulcus distinctly impressed laterally, more weakly so medially; anterior tentorial pits small, round. Mandibles abruptly narrowing over basal half, more gradually and evenly narrowing from midpoint to apex; outer surface strongly convex; mandibles strongly deflected ventrally, broadly exposing labrum. Antenna with 23–30 flagellomeres (27 in holotype), clearly varying with body length; first flagellomere slightly longer

than second, second subequal to third; first flagellomere roughly 3 × longer than wide, tenth flagellomere roughly 2 × longer than wide; apical flagellomere sharply pointed, but the tip not attenuate. Maxillary palps about equal in length to height of head.

Mesosoma (Figs 5–9) 1.25–1.35 × longer than high, 1.65–1.80 × longer than wide. Pronotum dorsally without median pit, crenulate along posterior margin, otherwise polished, unsculptured; pronotum laterally with dorsal, crenulate line extending as a broad, median groove to ventral corner, the groove crenulate for most of its length, though often more weakly so medially, posterior margin crenulate at least over ventral 0.5, area between posterior crenulate margin and median crenulate groove varying from weakly to moderately rugulose, pronotum laterally otherwise smooth and polished dorsoposteriorly and anteriorad median groove. Propleural flange large, distinct, sharply bent posteroventrally; separated from remainder of propleuron by oblique, weakly to strongly sculptured groove. Anterior declivity of mesoscutum densely covered with decumbent setae, setae extending onto base of disc, in 2–3 rows along notauli, and as a scattered patch of somewhat more erect setae between midpit and scutellar sulcus; notauli deeply impressed and sculptured on basal 0.4–0.5 of mesoscutum, abruptly to gradually transforming to very shallow, unsculptured depressions extending posteriorly and sometimes almost imperceptibly to oval or tear-drop shaped midpit; midpit covering apical 0.2 of disc, well separated from distinct transscutal articulation; carinate lateral margin of disc crenulate, deeply impressed between tegula and rugose base of notaulus. Scutellar sulcus about 4 × wider than length along midline; smooth, with 6–8 distinct ridges. Scutellum evenly convex, not strongly elevated; polished throughout, with scattered setae. Metanotum with small, low median tubercle. Propodeum densely rugose, the sculpture often somewhat weaker posteromedially, transverse carina varying from distinct to indistinct; propodeal spiracle minute, situated about midway between anterior and posterior margins; propodeum separated from metapleuron by a shallow to deep groove. Metapleuron broadly impressed and carinately rugose around margins; median plate varying from polished, punctate, and largely unsculptured to uniformly rugulose. Hind margin of mesopleuron crenulate throughout, though sometimes more weakly so dorsally, the crenulate impression forming nearly a straight line. Precoxal sulcus incomplete posteriorly, but extending most of way to mid coxa; gradually widening anteriorly, roughly twice as broad anteriorly as posteriorly; crenulate throughout; precoxal sulcus anteriorly joining broadly crenulate groove along anterior margin of mesopleuron and extending dorsally then posteriorly ventrad the setose subtegular ridge. Sternaulus crenulate throughout, nearly parallel to but distinctly separated from more dorsally positioned precoxal sulcus, slightly longer than the latter and of approximately uniform width throughout.

Fore wing (Fig. 14) with stigma broad, wedge-shaped: widest at origin of r, tapered into metacarpus distally; r arising from about basal 0.4, length of r 0.75–0.90 × width of stigma; second submarginal cell large, weakly converging distally, 5-sided with m-cu distinctly postfurcal, 2RS strongly reclivous, r-m slightly inclivous, completely depigmented and desclerotized; 3RSa 1.35–1.70 × longer than 2RS; 3RSb 1.45–1.60 × longer than 3RSa; 3RSb extending to wing margin very close to wing apex; RS+M weakly sinuate, nearly straight, arising low on almost evenly bowed 1M (the curvature slightly stronger posteriorly), 1RS 0.35–0.45 × length of 1M; large median bulla covering all of 2 Ma, posterior extremities of RS+M and 2RS, and anterior portion of m-cu; 3M tubular and distinctly pigmented for more than half its length; 1cu-a inclivous, separated from 1M by nearly its own length; 1st

subdiscal cell closed, 2CUa strongly inclivous, nearly twice length of tubular 2cu-a; 1-1A weakly bowed towards wing margin, separated near mid-length from the latter by about twice its width. Hind wing (Fig. 15) with RS represented by unpigmented, spectral crease; 2M and m-cu nearly always weakly but distinctly pigmented, m-cu strongly bowed with posterior end directed towards wing base; 2-1A absent.

Metasoma (Figs 10–13) with gaster in dorsal view broadly oval, distinctly tapering anteriorly and posteriorly. Petiole 1.0–1.3 × longer than apical width, apex 1.8–2.2 × wider than base; largely smooth, polished basal-medially, striate to strigose laterally and over entire apical half, dorsal carinae converging near mid-length but not quite touching, replaced by a low, median ridge over apical half; dorsope distinct, deep. Hypopygium weakly sclerotized and folded along midline; short, with posterior margin moderately protruding medially but apex not extending to tip of metasoma. Ovipositor protruding distinctly beyond metasoma, 1.4–1.5 × longer than mesosoma, upper valve with distinct subapical node, valve slightly narrowed immediately basad node; ovipositor sheath 0.85–0.95 × length of mesosoma, with tuft of long setae over apical third, 2 ventral and 1 lateral row of more widely spaced setae basally.

Color mostly dark brown; legs yellow, fifth tarsomere brown, apical 0.15–0.20 of posterior face of hind tibia and hind tarsi dorsally light brown in specimens from Rutshuru and those reared from *Psychotria* fruits in Kenya, brown infumation on tibia absent or very weakly indicated in specimens from Cameroon and those reared from *Strombosia* fruits in Kenya; flagellum brown to dark brown; scape, occasionally pedicel, most of mandible, labrum, palps, tegula, and pleural areas adjacent tegula yellow; apical margin of clypeus, posterior traces of notauli, extreme base of metasomal tergum 2, scutellum posteriorly, and often parts of metanotum reddish brown; metasomal terga and sterna otherwise dark brown in specimens from Rutshuru and *Psychotria* fruits in Kenya, the laterotergites lighter brown with pale margins, terga yellow brown and sterna pale in specimens from Cameroon, terga 2+3 with large, dark brown spot medially, remainder of metasoma dorsally and ventrally yellow; wings hyaline.

Length of body (exclusive of antenna and ovipositor) 2.5–3.6 mm; of wing 2.6–3.6 mm; of antenna about 3.1–4.3 mm.

Male as in female except as follows: antenna with 23–30 flagellomeres; petiole narrower apically, thus appearing more parallel-sided, 1.25–1.40 × longer than apical width, apex 1.5–1.8 × wider than base; body and wing length more variable, 1.8–3.4 and 2.0–3.3 mm respectively; specimens from Cameroon with antenna entirely yellow and metasomal terga 2+3 yellow brown with remaining terga brown; specimens reared from *Strombosia* fruits in Kenya also with antenna entirely yellow, but metasomal terga entirely dark brown. Fischer (1965) noted that in males, r was half the length of 2RS in the male paratypes and 2/3rds the length of 2RS in the female holotype; in the longer series examined here, most males had a slightly shorter r cross-vein than females, but the difference was smaller than in Fischer's material.

Biology.—Reared from larvae of the following Tephritidae (Diptera) infesting fruit of Moraceae (from *Ceratitis* MacLeay spp. infesting *Antiaris toxicaria* (Pers.) Lesch. in Kakamega forest, Kenya), Olacaceae (from *Ceratitis anonae* Graham and/or *C. fasciventris* (Bezzi) infesting *Strombosia scheffleri* Engl. in Kakamega), Sapotaceae (from *C. anonae* infesting *Englerophytum oblanceolatum* (S. Moore) T. D. Penn. in Kakamega) and Rubiaceae (from *Trirhithrum* Bezzi and/or *Ceratitis* infesting *Coffea* spp. for all Cameroon collections; from *Trirhithrum meladiscum* Munro infesting *Psychotria fractinervata* Petit in Gatamayu forest, Kenya and *P. mahonii* C.

Wright in Mt. Kenya forest; and from *T. senex* Munro infesting *P. alsophila* K. Schum. in Taita Hills, Kenya). See material examined section for details of localities. *Bactrocera amplexa* (Munro) was also present in the samples of *Strombosia*, but the isolated puparia from which wasps emerged were those of *Ceratitis*. Emergence, as in all known opiines, was from the host puparium. Host stage attacked is unknown.

Material examined.—Holotype female, DEMOCRATIC REPUBLIC OF THE CONGO Rutshuru, 29.v.1936 (L. Lippens) (MRAC).

Additional specimens: BURUNDI 1 male(?), Bururi, Urundi, 2200 m, 4.ix.1948 (François) (MRAC). CAMEROON 2 males, Akonolinga, viii.1982 (G. Steck), TAMU Quarantine # 82-31, TAMU Voucher # 82; 2 females, 3 males, Nkolbisson, x.1982 (G. Steck), TAMU Quarantine #s 82-39 to 82-41, TAMU Voucher #s 87 to 89; 1 male, same locality, 1980 (Perkins) (TAMU). DEMOCRATIC REPUBLIC OF THE CONGO 2 females, 2 males, same locality as holotype, ix–x.1936 & 7.iv.1937 (MRAC). KENYA 4 females, 4 males, Central Province, Gatamayu forest, 0°58.45′S, 36°41.83′E, 17.iv.2001 & 19.x.2001 (R. Copeland); 1 male, Coast Province, Ngangao forest, Taita Hills, 3°21.255′S, 38°20.579′E, 12.viii.2002 (R. Copeland & R. Wharton); 2 females, 2 males, Eastern Province, Mt. Kenya forest, 0°12.568′S, 37°30.218′E, 6.xii.2001 (R. Copeland); Western Province, Kakamega forest, 4 females, 3 males, 0°14.16′N, 34°51.82′E, reared from *Ceratitis* infesting fruits of *Strombosia scheffleri*, 30.iv.2000 (R. Copeland); 1 male, 0°13.14′N, 34°53.76′E, reared from *Trirhithrum senex* infesting fruits of *Englerophytum oblanceolatum*, 7.vi.2001 (R. Copeland);1 female, 1 male, 0°14.16′N, 34°51.87′E, reared from *Ceratitis* infesting fruits of *Antiaris toxicaria*, 3.iii.2000 (R. Copeland); 1 male, same but 0°13.66′N, 34°53.12′E, 19.ii.2001 (TAMU, National Museums of Kenya).

Diagnosis.—This species is similar to *Sternaulopius duplicatus* **new species**, *Biophthora rossicus* (Szépligeti) **new combination**, and *B. bajulus* **new status**, in the possession of both a sculptured sternaulus and a sculptured precoxal sulcus. It differs from these species by its more broadly exposed labrum and long ovipositor with distinct subapical node.

Remarks.—In overall appearance (body shape, size, and fore wing venation), *S. bisternaulicus* resembles species of *Utetes*, but has a distinct dorsope and lacks the sharp carina on the base of the inner side of the hind tibia that characterizes members of the genus *Utetes*. Since species of both genera have occasionally been reared from tephritids infesting the same host fruits, and both lack the attenuate hypopygium of many of the other parasitoids of fruit-infesting tephritids, careful attention needs to be paid to these distinguishing characteristics in order to avoid misidentifications.

The most obvious difference between *bisternaulicus* and the two other species treated in detail here (*duplicatus* and *bajulus*) is the more broadly exposed labrum formed by the ventrally deflected mandibles. Compared to *bajulus*, both *bisternaulicus* and *duplicatus* have an evenly and weakly convex, dorsally unsculptured scutellum, a more broadly impressed anterior margin of the metapleuron and a distinctly longer fore wing cross-vein r. Minor differences between these two and *bajulus* include a straighter carinate groove on the posterior margin of the mesopleuron and somewhat coarser propodeal and mesopleural sculpture.

There is considerable morphological variation amongst the material available for examination, but I am unable to delineate more than a single species. Though not entirely satisfactory, I consider all of the specimens in the material examined section as representing a single, variable species because the series reared from *Trirhithrum meladiscum* infesting *Psychotria* fruits in central Kenya encompasses most of the range of variation observed in the rest. More specifically, the larger specimens reared from *Strombosia* fruits in western Kenya have slightly larger ocelli, and consequently a broader ocellar field.

Individuals reared from *Psychotria* fruits in various Kenyan localities, as well as individuals from Cameroon, have somewhat smaller ocelli as in the specimens from Rutshuru. Specimens from Cameroon tend to have more extensive, better-developed sculpture on the pronotum laterally and a more consistently deep and heavily sculptured oblique groove on the propleuron than the larger individuals reared from *Strombosia* fruits in western Kenya. Individuals reared from *Psychotria* fruits in central Kenya are highly variable in this regard, covering the extent of variation seen in all other populations. The setae on the median mesoscutal lobe extend further posteriorly in specimens from Cameroon than in the others, but in these the mesoscutum is still distinctly less setose than in the new species described below. The propodeal sculpture is much weaker posteriorly in most of the specimens from Cameroon and the Kenyan material reared from *Strombosia* fruits. The transverse carina is also distinct and readily visible in these specimens. The material from Rutshuru and most of the specimens reared from *Psychotria* fruits in Kenya are densely sculptured throughout, and as a consequence, the transverse carina is usually indistinct. However, there is some variation within localities and in particular the large series from *Psychotria* fruits contains some individuals with weaker propodeal sculpture and a couple of the males from Cameroon have denser sculpture posteriorly. The sternaulus is a little broader throughout in Cameroon and *Strombosia* material than in Rutshuru and *Psychotria* material, but is of the same length and very well developed in both groups. The second submarginal cell is similarly shaped in all populations, but extreme within-population variation in length of 2RS resulted in the broad range for the 3RSa/2RS ratio noted in the above description. Variation in the shape of the petiole, on the other hand, is partly a function of the difficulty in accurately measuring this structure on intact specimens and the slightly longer, narrower petiole of the Rutshuru specimens. Perhaps the most distinctive difference among the material examined is in coloration, with specimens from Rutshuru and from *Psychotria* and *Englerophytum* fruits in Kenya darker than specimens from Cameroon and from *Strombosia* and *Antiaris* fruits in Kenya. Thus, both lighter and darker forms can be found in Kakamega forest in western Kenya.

The species is distributed across equatorial Africa from coastal Kenya to Cameroon. The type material of *bisternaulicus* is from Rutshuru, in the eastern portion of present day Democratic Republic of the Congo, near the Uganda border.

The medially desclerotized hypopygium is reminiscent of some Cardiochilinae and Microgastrinae and similar in this respect to the equally short hypopygium found in fruit-infesting tephritid parasitoids of the genus *Utetes*. The functional significance is unknown.

Sternaulopius duplicatus Wharton, new species

(Figs 33–35)

Head in dorsal view 1.85–2.00 × broader than long, 1.50–1.55 × broader than length in lateral view, eyes weakly bulging beyond temples; face 1.30–1.45 × wider than high; eye in lateral view large, 3.35 (female) and 2.90 (male) × longer than temple. Frons, vertex, and occiput as in *bisternaulicus* except median sculpture on frons confined to area immediately posteriad antennal bases; face (Fig. 33) distinctly punctate on either side of polished, narrow midridge about as in *bisternaulicus* but with 1–2 distinct vertical rows of more closely-set punctures on either side of midridge in addition to the irregular pattern of punctures. Ocelli smaller than in most individuals of *bisternaulicus*; width of ocellar field 1.05–1.10 × distance from lateral ocellus to eye; width of ocellar field 2.2–2.5 × width

Figs 33–35. *Sternaulopius duplicatus*, n. sp., holotype female: 33, face. 34, anterior-dorsal view of mesonotum. 35, lateral habitus, arrow = precoxal sulcus.

of lateral ocellus. Hypostomal and occipital carinae as in *bisternaulicus*. Malar space short but distinct, 0.15–0.20 × eye height, a little shorter than basal width of mandible; region of malar space sculptured as in *bisternaulicus*. Clypeus (Fig. 33) a little taller and more oval in male than female, appearing truncate below in both depending on angle of view; nearly flat in profile; uniformly setose and punctate, distinctly but more sparsely punctate than in *bisternaulicus*; epistomal sulcus impressed laterally, barely indicated medially; anterior tentorial pits round, a bit larger than in *bisternaulicus*. Mandibles gradually and evenly narrowing from base to apex; about 3 × longer than median width; outer surface very weakly convex, nearly flat; mandibles barely deflected ventrally, completely concealing labrum when closed (Fig. 33). Antennae broken in both specimens, male with 25 flagellomeres remaining, female with 18; first flagellomere slightly longer than second, second slightly longer than third; first flagellomere roughly 3.5 × longer than wide, tenth flagellomere more than twice longer than wide and longer in male than female. Maxillary palps curled and length difficult to estimate but appear slightly shorter than in *bisternaulicus*.

Mesosoma (Figs 34, 35) 1.35 × longer than high, 1.75 × longer than wide. Pronotum not visible dorsally; laterally as in *bisternaulicus*. Propleural flange distinct, bent posteroventrally; separated from remainder of propleuron by oblique, weakly to strongly sculptured groove. Anterior declivity of mesoscutum densely covered with decumbent setae, these extending onto disc, covering entire median mesoscutal lobe and anterior and median portions of lateral lobes (Fig. 34), though not as densely as on anterior declivity; notauli weaker than in *bisternaulicus*, impressed and weakly sculptured on basal 0.2–0.3 of mesoscutum, faintly indicated medially, imperceptible posteriorly; midpit small, round, deep, separated from distinct transscutal articulation; carinate lateral margin of disc crenulate, deeply impressed between tegula and rugose base of notaulus. Scutellar sulcus a bit narrower medially than in *bisternaulicus*, about 5.6 × wider than length along midline; smooth, with 6–8 distinct ridges. Scutellum and metanotum as in *bisternaulicus*. Propodeum densely rugose; propodeal spiracle minute, situated about midway between anterior and posterior margins; propodeum separated from metapleuron by a shallow groove. Metapleuron broadly impressed and carinately rugose around margins; median plate polished and largely unsculptured. Hind margin of mesopleuron crenulate throughout, the crenulate impression forming nearly a straight line. Precoxal sulcus incomplete posteriorly, but extending most of distance to mid coxa; crenulate and of uniform width throughout; precoxal sulcus anteriorly as in *bisternaulicus*. Sternaulus crenulate throughout, nearly parallel to but distinctly separated from more dorsally positioned precoxal sulcus (the two grooves slightly converging posteriorly), slightly longer than precoxal sulcus and of approximately uniform width throughout.

Fore wing stigma about as in *bisternaulicus* but a little more gradually tapered distally; r appearing to arise more proximally, from basal 0.30–0.35; second submarginal cell, m-cu, r-m, 1M, 1RS, 2RS, 3M, 1-1A, and median bulla as in *bisternaulicus*; 3RSa about 1.70 × longer than 2RS; 3RSb 1.55–1.60 × longer than 3RSa; 3RSb extending to wing margin very close to wing apex; RS+M straight to nearly so; 1cu-a vertical to nearly vertical, separated from 1M by half its length or slightly less; 1st subdiscal cell about as in *bisternaulicus* but 2cu-a longer, distinctly more than half length of 2CUa. Hind wing about as in *bisternaulicus* but m-cu shorter, straighter, and more weakly pigmented than in most individuals of the latter; 2-1A absent.

Metasoma with gaster in dorsal view broadly oval, distinctly tapering anteriorly

and posteriorly. Petiole 1.35 (female) and 1.60 (male) × longer than apical width, apex 1.6 × wider than base in male, base not completely visible in female; striate to strigose except in basal depression, dorsal carinae extending to apex though weaker posteriorly, weakly converging throughout length; dorsope as in *bisternaulicus*. Hypopygium short, not extending to tip of metasoma; shape about as in *bisternaulicus* but difficult to discern because of deflected ovipositor. Ovipositor about 0.75 × length of mesosoma, upper valve without distinct subapical node; ovipositor sheath about 0.35 × length of mesosoma, with tuft of long setae apically, and more widely spaced setae basally.

Color mostly dark brown to black; scape, clypeus, palps, tegula, base of metasomal tergum 2 and legs yellow, the coxae and trochanters more pale in male; mesosoma dark brown to black dorsally and ventrally, with small reddish patches laterally in female, male more extensively reddish to reddish-yellow; petiole reddish brown, terga 2+3 yellow-brown to reddish brown, remaining metasomal terga dark brown; wings hyaline or nearly so.

Length of body (exclusive of antenna and ovipositor) about 2.3 mm; of wing 2.6–2.7 mm.

Material examined.—Holotype female MADAGASCAR. Label with 4 lines as follows: "COLL. MUS. CONGO", "Madagascar: Ankaratra", "IV-1944" and "A. Seyrig" (deposited in MRAC).

Paratype male MADAGASCAR same label data as holotype (MRAC).

Diagnosis.—This species is characterized by the presence of both a sculptured sternaulus and sculptured precoxal sulcus, a combination known only in *Sternaulopius* and *Biophthora* among the Opiinae. *Sternaulopius duplicatus* lacks the elevated, dorsally sculptured scutellum of the species placed in *Biophthora* below, and is most readily differentiated from the only other valid species of *Sternaulopius*, *S. bisternaulicus*, by the shorter ovipositor, more densely setose mesoscutum, and concealed labrum.

Remarks.—The concealed labrum of this species makes it more challenging to argue for the exclusion of *bajulus* from *Sternaulopius* since the differences in appearance of the clypeus and mandibles between *duplicatus* and *bajulus* are relatively minor. As noted above in the general discussion under *Sternaulopius*, recognition of *Biophthora* as a separate genus is based primarily on the nature of the scutellum and in this *duplicatus* and *bisternaulicus* are markedly different from *bajulus*. Other essential features that assist in the placement of *duplicatus* in *Sternaulopius* rather than *Biophthora* are found in the details of sculpturing of the malar region, mesopleuron, and propodeum as well as the punctation and shape of the clypeus. See further remarks under *bisternaulicus*.

The length of the ovipositor and sheath given in the above description are estimates since the holotype was not dissected. However, since the base of the ovipositor is partially exposed in the holotype, the estimate is fairly accurate. The ovipositor of this species is thus considerably shorter than in *bisternaulicus*, and at rest probably protrudes only slightly beyond the apex of the metasoma. As in *bajulus*, there is no discernible subapical node on the dorsal valve in *duplicatus* suggesting that *duplicatus* may oviposit into an earlier host stage than *bisternaulicus*.

If the presence of a sternaulus (in addition to the precoxal sulcus) is overlooked, *duplicatus* runs to *Opius* (*Frekius*) *castaneus* Granger in the keys to Opiinae published by Granger (1949) and Fischer (1972, 1987). *Opius castaneus* is the type species of *Frekius* Fischer, 1971b. The holotype of *castaneus* lacks a sternaulus but surprisingly the hind tibia is carinate basally as in *Utetes*. I therefore transfer Granger's species to *Utetes* where the **new combination** is *Utetes* (*Frekius*) *castaneus* (Granger). I retain, at least temporarily, the name *Frekius* as a valid subgenus pending

a badly needed revision of the genus *Utetes*. Typical *Utetes* have a broadly exposed labrum and thus the inclusion of *Frekius* in *Utetes* is not without problems since *castaneus* does not have an exposed labrum. The parallels between *Utetes* and *Sternaulopius* in the unusually variable nature of the labral exposure are also deserving of closer attention.

Sternaulopius duplicatus is known from only two specimens; the species name refers to the two parallel grooves on the mesepisternum (precoxal sulcus and sternaulus).

Biophthora bajulus (Haliday, 1837)

(Figs 16–20)

Opius bajulus Haliday, 1837: 214; Marshall 1891: 43, redescription, key, English; Marshall 1894: 327–328, redescription, key, French; Dalla Torre 1898: 59, catalog; Szépligeti 1904: 164, checklist; Fischer 1958: 58–60 redescription, keys; Fischer 1971a: 46, catalog; Papp 1981b: 35, key; Tobias and Jakimavicius 1986: 96–97, key, figures; Belokobylskij et al. 2003: 393, checklist, clarification of date of original description in this and other 19th century publications relevant to Opiinae.

Biophthora bajulus: Foerster 1862: 260.

Sternaulopius beieri Fischer, 1968: 103–105, **new synonym**; Fischer 1971a: 125, catalog; Fischer 1972: 478–479, redescription; Papp 1981a: 273–274, distribution, diagnosis; Papp 1981b: 135, redescription, key; Quicke et al. 1997: 25–36, venom glands, relationships; Tobias 1998: 559–561, key; Belokobylskij et al. 2003: 396, checklist; Yu and van Achterberg 2005, electronic catalog.

Opius (*Xynobius*) *bajulus*: Fischer 1972: 88–90, redescription, key, figures; Tobias and Jakimavicius 1986: 29, key, figures.

Xynobius bajulus: van Achterberg, 1997: 18, original description listed as published in 1836, following Horn and Schenkling (1928); van Achterberg 2004: 315.

Redescription.—Head in dorsal view 1.8–1.9 × broader than long, 1.3–1.4 × broader than length in lateral view, as wide at temples as at eyes; face (Fig. 18) 1.7–1.8 × wider than high; eye in lateral view 1.2–1.3 × longer than temple. Face (medially), vertex, frons and occiput polished; low median ridge present from epistomal sulcus to level of antennal bases, replaced by shallow groove on frons; face sparsely and finely punctate medially, punctures separated by at least their own diameter, weakly rugulose and dull (unpolished) adjacent eye margin; frons with 3–5 setae along eye margin, otherwise bare and unsculptured; vertex sparsely setose. Ocelli and ocellar field small, width of ocellar field 0.70–0.75 × distance between lateral ocellus and eye; width of ocellar field 3.0–3.4 × width of lateral ocellus. Hypostomal carina protruding as a short but distinct flange beneath mandible when mandible closed; occipital carina very widely separated from hypostomal carina ventrally (by a distance greater than basal width of mandible), relatively short, extending dorsally just above middle of eye in lateral view, not reflected medially at dorsal terminus, broadly curved in lateral view due to prominantly swollen gena. Malar space broad, 0.3–0.4 × eye height, about equal to basal width of mandible; rugulose-strigose (Fig. 18), with sculpture extending from malar sulcus to ventral-lateral margin of clypeus; malar sulcus complete from eye to subgenal margin but barely distinguishable from adjacent sculpture. Clypeus broadly hemi-elliptical, truncate and sharpy margined ventrally, punctate and setose along dorsal margin, otherwise polished and bare; epistomal sulcus distinctly impressed throughout, though slightly less so medially; anterior tentorial pits narrow, slit-like. Mandible gradually and evenly narrowing from base to apex; slightly more than twice longer than basal width but less than 3 × longer than median width; weakly deflected ventrally, exposing labrum in a narrow but distinct gap between clypeus and mandibles when the latter are closed (Fig. 18). Antenna with 24–26 flagellomeres; first flagellomere slightly longer than second; apical flagellomere sharply pointed, but tip not attenuate.

Maxillary palps shorter than height of head.

Mesosoma (Figs 17, 19, 20) 1.2–1.3 × longer than high, 1.8–1.9 × longer than wide. Pronotum dorsally without median pit, crenulate along posterior margin, otherwise polished, unsculptured; pronotum laterally finely sculptured throughout except largely smooth anteriorad median groove. Propleural flange large, distinct, sharply bent posteroventrally; separated from remainder of propleuron by oblique, strongly sculptured groove. Anterior declivity of mesoscutum densely covered with decumbent setae; disc bare except for scattered row of setae along each notaulus and on either side of midpit; notauli extending onto anterior 0.4 of disc as crenulate grooves, abruptly transforming to shallow, unsculptured depressions extending posteriorly to narrow, slit-like midpit, largely to completely obscured at base by rugose sculpture; midpit (Fig. 19) weakly sculptured, covering apical 0.25 of disc, extending to barely perceptible transscutal articulation; lateral margin of mesoscutum crenulate, deeply impressed between tegula and rugose base of notaulus. Scutellar sulcus about 4–5 × wider than length along midline, with 6–8 ridges partially obscured by rugulose sculpture. Scutellum (Fig. 19) arising vertically from posterior margin of scutellar sulcus, distinctly elevated above plane of mesoscutum; dorsal surface flattened, densely rugose throughout, with sculpture extending to metanotum. Metanotum with small, low median tubercle. Propodeum (Fig. 19) densely and finely rugose, the sculpture somewhat weaker posterior-medially, transverse carina weak, barely discernible; propodeal spiracle minute, situated about midway between anterior and posterior margins; propodeum separated from metapleuron by a shallow groove margined medially by a low carina posteriorly. Metapleuron narrowly impressed and carinately rugose around margins; median plate polished, punctate, and largely unsculptured. Hind margin of mesopleuron finely crenulate throughout, the crenulate impression emarginate near middle. Precoxal sulcus (Figs 17, 19) incomplete posteriorly, extending slightly more than half distance from anterior margin to mid coxa; finely crenulate throughout, weakly tapered posteriorly; precoxal sulcus weakly separated from crenulate groove along anterior margin of mesopleuron or connected to groove only as a faint trace; anterior margin of mesopleuron finely crenulate, the sculpture extending posteriorly ventrad subtegular ridge, with a few weak striae extending ventrally towards middle of mesopleuron from subtegular ridge. Sternaulus (Figs 17, 19) finely crenulate throughout, parallel to but distinctly separated from more dorsally positioned precoxal sulcus; of uniform width throughout. Midventral groove crenulate; postpectal carina completely absent.

Fore wing stigma broad, wedge-shaped: widest at origin of r, tapered into metacarpus distally; r arising from basal 0.35, r short, at most half as long as width of stigma; size and shape of second submarginal cell as in *bisternaulicus*; m-cu distinctly postfurcal, r-m and 2Ma slightly more distinct than in most specimens of *bisternaulicus*, due to trace of pigmentation; 3RSa 1.65–1.75 × longer than 2RS; 3RSb 1.2–1.3 × longer than 3RSa; 3RSb extending to wing margin near tip but not as close to apex as in *bisternaulicus* and *duplicatus*; RS+M weakly but distinctly sinuate, arising low on almost evenly bowed 1M (the curvature slightly stronger posteriorly), 1RS 0.30–0.35 × length of 1M; 3M tubular and distinctly pigmented for slightly less than half its length; 1cu-a vertical to very weakly inclivous, separated from 1M by about 0.5–0.7 × its length; 1st subdiscal cell closed, 2CUa strongly inclivous, distinctly longer than tubular 2cu-a; 1-1A weakly bowed towards wing margin, separated near mid-length from the latter by nearly 3 × its width. Hind wing (Fig. 16) as in *bisternaulicus* except m-cu not so strongly

curved, nearly reaching wing margin and 2-1A short but distinct.

Metasoma (Fig. 17) with gaster in dorsal view nearly parallel-sided, gradually tapering posteriorly. Petiole short, length 0.85–0.95 × apical width; 2.35–2.45 × wider at apex than at base; sparsely striate to strigose (Fig. 19), dorsal carinae distinct basally, difficult to distinguish from surrounding sculpture apically, apparently extending to apex, not converging; dorsope small, round, deep. Spiracle of second metasomal tergum positioned as in *bisternaulicus*, dorsad and nearly adjacent lateral crease of median tergite. Hypopygium short, apex not extending to tip of metasoma. Ovipositor very short, not extending beyond apex of metasoma, upper valve without subapical node; ovipositor sheath about 0.25 × length of mesosoma, with tuft of long setae apically.

Head and mesosoma dark brown to black; tegula, metasoma and coxae dark reddish brown, fore coxa sometimes more yellowish; tarsomeres 5 and sometimes 4 dark brown, remainder of legs dark yellow; clypeus and mandibles yellow; palps light brown; wings hyaline or nearly so.

Length of body (exclusive of antenna and ovipositor) about 2.6–2.7 mm; of wing 2.8–2.9 mm; of antenna 3.0–3.1 mm.

Material examined.—Holotype female of *bajulus*, ENGLAND (Walker) (NMID). Van Achterberg (1997) noted that the holotype of *bajulus* is a female but was listed in the original description as a male probably because the genitalia are not readily visible.

Holotype female of *beieri*, GERMANY "Sachsen Altenbach bei Wurzen Coll. Dr. R. Krieger 31.5.93" (ZMHB).

Additional specimens: 1?, AUSTRIA, Thüringen (NHMW); CZECH REPUBLIC, 1?, Hrádek (NHMW); 1?, Moravia, Brno (NHMW); 1 female, IRELAND, County Kildare, R. Canal, 18.vi.1944 (Stelfox) (USNM).

Distribution.—Previously recorded from Czech Republic, Denmark, Germany, Hungary, England, Ireland, and Turkey (Fischer 1971a, Papp 1981a, Quicke et al. 1997). The specimen noted above from Thüringen in NHMW is assumed to be from Austria but this new record needs verification. The holotype female of *beieri* has the date hand-written sideways on the label, "Sachen" and "Dr. R. Krieger" printed, and the specific locale hand-written and difficult to read. Fischer (1968) interpreted the specific locality as Altenberg, which was a well-known locality in Saxony of that time period. However, there was also a small village called Altenbach just east of Leipzig near Wurzen, and I interpret the label to read Altenbach rather than Altenberg. Data on the holotype of *bajulus* are provided by Marshall (1891) and van Achterberg (1997).

Diagnosis.—*Biophthora* is readily recognized by the presence of both a sculptured sternaulus and a sculptured precoxal sulcus in addition to the rugose dorsal surface of the elevated scutellum and a deep dorsope. The scutellar feature separates *bajulus* from members of the genus *Sternaulopius*, but not from *Biophthora rossicus* (Szépligeti, 1901), **new combination**, which is nearly identical to *bajulus* (including the presence of a true sternaulus). The holotype of *rossicus* (HNHM) has the notauli better developed than in specimens I have seen of *bajulus* (including *beieri*).

Remarks

I exclude *bajulus* from *Sternaulopius*, despite the presence in *bajulus* of both a crenuate sternaulus and a sculptured precoxal sulcus; *bajulus* differs from the species of *Sternaulopius* by the more rugose malar region, the more parallel-sided metasoma, and in particular the sculpture and shape of the scutellum. The presence of a true sternaulus in *bajulus* is hypothesized as a case of remarkable convergence with the condition in *Sternaulopius*. The sternaulus of *bajulus*, though distinct when not obscured by glue or the position of the legs (as is often the case), is decidedly finer and weaker than in *bisternaulicus* and *duplicatus*. See remarks section under the genus *Ster-*

naulopius for rationale regarding recognition of *Biophthora* and placement of *bajulus* therein.

The synonymy between *beieri* and *bajulus* has undoubtedly been overlooked because few specimens have been available for study and the sternaulus in *bajulus* is difficult to see relative to the better developed sternaulus in *bisternaulicus*. Thus, both Fischer (1972) and van Achterberg (2004) placed *bajulus* in *Xynobius* on the basis of more readily visible characters such as the sculptured scutellum and the dorsope. Compared to other species placed in *Xynobius*, *bajulus* has a more completely concealed labrum, with the clypeus broader, flatter, truncate and not as sharply margined ventrally and the mandibles are flatter and less strongly narrowed from base to apex. The fore wing venation is very different from that of typical *Xynobius* due to the shape of the stigma, the postfurcal m-cu, the relatively short 1M, the strongly reclivous 2RS and less strongly bowed 1-1A. Except for the notably shorter cross-vein r, the fore wing of *bajulus* is identical in all important respects to that of *bisternaulicus* and *duplicatus*.

The present study focuses on the morphological differences and similarities amongst *Biophthora*, *Eurytenes s. l.*, and *Sternaulopius*, but does little to resolve their phylogenetic relationships, either relative to one another or within the Opiinae as a whole. Quicke et al. (1997), using venom gland morphology to assess relationships amongst a wide variety of opiine and alysiine braconids, suggested a relationship between *beieri* and various species of *Xynobius* based on venom gland apparatus of a specimen from Denmark. The utility of the tripartite reservoir and notably small glands will need to be reassessed now that the classification has been considerably altered, especially since the glands of *caelatus* were not examined. Nevertheless, the hypothesis of a close relationship between *Biophthora* and *Eurytenes s. l.* cannot be rejected and is deserving of more detailed study as is the possible relationship between *Sternaulopius* and *Utetes*.

The differences noted by Wharton (1988) between *bisternaulicus* and *bajulus* relative to hind wing RS and m-cu have not held up upon examination of more material, though another potentially useful character (presence vs. absence of 2-1A) has been discovered. The ovipositor and sheath of *bajulus* are distinctly shorter than in *bisternaulicus*, and also appear to be shorter than in *duplicatus*. Although the ovipositor is very short in *bajulus*, the exact length could not be measured accurately on the available material.

Papp (1981a) has provided some additional features for separation of *bajulus* (as *beieri*) from *rossicus*. Since the holotype and only known specimen of *rossicus* is male and *bajulus* is rare, the separation of the two species will eventually need to be examined in more detail.

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